

# Neotropical Monogenoidea. 47. Phylogeny and coevolution of species of *Rhinoxenus* (Platyhelminthes, Monogenoidea, Dactylogyridae) and their Characiformes hosts (Teleostei, Ostariophysi) with description of four new species

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## ABSTRACT

Eight species of *Rhinoxenus* are reported from nasal cavities of characiform fishes in the Neotropics: *Rhinoxenus arietinus* Kritsky, Boeger & Thatcher, 1988, from anostomid hosts; *R. bulbovaginatus* Boeger, Domingues & Pavanelli, 1995, from characid hosts; *R. nyttus* Kritsky, Boeger & Thatcher, 1988, from anostomid hosts; *R. piranhus* Kritsky, Boeger & Thatcher, 1988, from serrasalmin hosts; *R. anaclaudiae* n. sp., from characid hosts; *R. euryxenus* n. sp., from serrasalmin and anostomid hosts; *R. curimbatae* n. sp., from prochilodontids hosts; and *R. guianensis* n. sp., from curimatid hosts. Furthermore, several undeterminate species are reported from *Hydrolicus scomberoides* (Cynodontidae). Hosts were collected from rivers in Brazil and French Guiana. The hypothesis on the sister-group relationships of species of *Rhinoxenus* (C.I. = 66%; R.I. = 66%), based on 10 transformation series, is ((*R. nyttus*, *R. curimbatae* n. sp.) (*R. bulbovaginatus* (*R. arietinus* (*R. guianensis* n. sp., *R. anaclaudiae* n. sp. (*R. euryxenus* n. sp., *R. piranhus*))))). Coevolutionary analysis suggests that events of cospeciation, duplication, dispersion, and extinction are required to explain the observed host-parasite association. The origin of *R. curimbatae* n. sp., *R. nyttus*, *R. bulbovaginatus*, *R. anaclaudiae* n. sp., and the ancestor of *R. piranhus* + *R. euryxenus* n. sp. are putatively associated with events of cospeciation with the ancestors of their respective host families. Dispersion with subsequent allopatric speciation to Anostomidae and Curimatidae appear associated with the origins of *R. arietinus* and *R. guianensis* n. sp., respectively. Extinction is necessary to explain the absence of *Rhinoxenus* spp. on several other characiform families, although sampling density cannot be discarded.

## KEY WORDS

Platyhelminthes,  
Monogenoidea,  
Dactylogyridae,  
Ancyrocephalinae,  
Characiformes,  
phylogeny,  
coevolution,  
new species.

## RÉSUMÉ

*Monogenoidea néotropicaux. 47. Phylogénie et coévolution des espèces de Rhinoxenus (Plathelminthes, Monogenoidea, Dactylogyridae) et de leurs hôtes Characiformes (Teleostei, Ostariophysi) et description de quatre nouvelles espèces.*

Huit espèces de *Rhinoxenus* sont rapportées des cavités nasales de poissons characiformes de la région néotropicale : *Rhinoxenus arietinus* Kritsky, Boeger & Thatcher, 1988, chez des Anostomidae ; *R. bulbovaginatus* Boeger, Domingues & Pavanelli, 1995, chez des Characidae ; *R. nyttus* Kritsky, Boeger & Thatcher, 1988, chez des Anostomidae ; *R. piranhus* Kritsky, Boeger & Thatcher, 1988, chez des Serrasalminae ; *R. anaclaudiae* n. sp., chez des Characidae ; *R. euryxenus* n. sp., chez des Serrasalminae et des Anostomidae ; *R. curimbatae* n. sp., chez des Prochilodontidae ; et *R. guianensis* n. sp., chez des Curimatidae. De plus, plusieurs espèces indéterminées de *Rhinoxenus* sont rapportées chez *Hydrolicus scomberoides* (Cynodontidae). Les hôtes ont été récoltés dans des rivières du Brésil et de Guyane française. L'hypothèse sur les relations phylogénétiques des espèces de *Rhinoxenus* (C.I. = 66 % ; R.I. = 66 %), basée sur 10 séries de transformations, est : ((*R. nyttus*, *R. curimbatae* n. sp.) (*R. bulbovaginatus* (*R. arietinus* (*R. guianensis* n. sp., *R. anaclaudiae* n. sp. (*R. euryxenus* n. sp., *R. piranhus*))))). L'analyse coévolutive suggère que des événements de cospéciation, duplication, dispersion et extinction sont requis pour expliquer l'association hôte-parasite observée. Nous faisons l'hypothèse que l'origine de *R. curimbatae* n. sp., *R. nyttus*, *R. bulbovaginatus*, *R. anaclaudiae* n. sp. et l'ancêtre de *R. piranhus* + *R. euryxenus* n. sp. sont associés à des événements de cospéciation avec des ancêtres de leurs familles d'hôtes respectives. La dispersion avec une spéciation allopatrique subséquente vers les Anostomidae et des Curimatidae semble avoir été associée avec l'origine de *R. arietinus* et *R. guianensis* n. sp., respectivement. L'extinction est nécessaire pour expliquer l'absence de *Rhinoxenus* spp. chez plusieurs autres familles de Characiformes, bien qu'un biais dû à l'échantillonnage ne puisse être écarté.

## MOTS CLÉS

Plathelminthes,  
Monogenoidea,  
Dactylogyridae,  
Ancyrocephalinae,  
Characiformes,  
phylogénie,  
coévolution,  
nouvelles espèces.

## INTRODUCTION

Characiformes (*sensu* Fink & Fink 1981) is divided into 16 (Greenwood *et al.* 1966) or 14 families (Géry 1977) with species endemic to Africa (four families; about 200 species) and the Neotropics (12 families; more than 1200 species) (Ortí & Meyer 1997). The most important advances in the systematics of the group occurred during the latter part of the 19th and much of the 20th century. Some of the advances were based primarily on anatomical features, which lacked a rigorous analytical method, resulting in many divergent classifications and largely untestable hypotheses on the evolutionary history of the group (Vari 1998). However, the application of phylogenetic

methods and the use of other systems of characters (e.g., molecular, cytogenetic) resulted in more stable phylogenies, based on testable hypotheses. Vari (1998) provides an overview of the phylogenetic concepts utilized for proposal of the major lineages within what is now recognized as the order Characiformes.

Species of *Rhinoxenus* Kritsky, Thatcher & Boeger, 1988 are all parasites of the nasal cavity of characiform fishes. Boeger *et al.* (1995) suggest that these species comprise a monophyletic group with the origin of their species associated with the divergence of ancestor species of their hosts. This suggests the possible usefulness of these parasites as evolutionary markers for the sister-group relationships of the families of their characiform

hosts. Thus, this study tests the hypothesis of Boeger *et al.* (1995) by re-evaluating the hypothesis of cospeciation by the inclusion of new species described herein and a re-evaluation of the morphological matrix.

## MATERIAL AND METHODS

Fish hosts were collected from Brazil and French Guiana. A list of necropsied species for this study with collection data and number of examined specimens is presented in the Appendix. Methods of parasite collection, preparation, measurement, and illustration follow Kritsky *et al.* (1986, 1988). Measurements are in  $\mu\text{m}$ . Type specimens and vouchers are deposited in the parasite collections of the Coleção Helmintológica do Instituto Oswaldo Cruz, Rio de Janeiro, RJ, Brazil (CHIOC); the Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil (INPA); Muséum national d'Histoire naturelle, Paris, France (MNHN); Museu de Zoologia, Universidade de São Paulo (MZUSP); and the U.S. National Museum, Helminthological Collection, Beltsville, Maryland, USA (USNPC), as indicated in the respective descriptions.

The phylogenetic relationship of *Rhinoxenus* spp. is determined using techniques of phylogenetic systematics (*sensu* Hennig 1966). The transformation series and character states were defined based on the literature or through the study of voucher and type specimens. An initial hypothesis on evolutionary relationships of *Rhinoxenus* species was constructed manually using Hennigian Argumentation (Wiley 1981) and tested with the program PAUP\* 4.0b10 (Swofford 2002) using HSEARCH, unlimited MAXTREE, and 1000 random addition sequence (set maxtrees = 10000, increase = auto, hsearch addseq = random, hold = 2, nreps = 1000, rstatus = yes) to confirm that the tree obtained was a most-parsimonious tree. Bootstrap values were calculated based on 1000 replicates and were considered supportive when  $\geq 50\%$ . A strict consensus cladogram was developed to evaluate branch support from all most-parsimonious trees. All transformation series were considered initially unordered and were

polarized and optimized according to the techniques described by Watrous & Wheeler (1981) and Maddison *et al.* (1984). *Protorhinoxenus prochilodi* Domingues & Boeger, 2002 was used as outgroup (Domingues & Boeger 2002).

The coevolutionary analysis was performed using BPA (Brooks Parsimony Analysis) as described by Brooks (1981, 1990), Brooks & McLennan (1991, 1993) and Brooks *et al.* (2001). The host cladogram used is that proposed by Buckup (1993, 1998). *Triportheus* and *Salminus* are included in Characoidea (*sensu* Buckup 1998) based on their relationship with *Brycon*, as suggested by Malabarba (1998). Only taxa reported as hosts of *Rhinoxenus* spp. or scrutinized in this study were included in the cladogram. The parasite phylogeny was transformed into a matrix by additive binary coding; each parasite species was coded as to indicate both its identity and ancestor (evolutionary history). A matrix for the host groups was then constructed based on this parasites coding based on the parasites distribution (Table 10); hosts without parasites were coded by missing or inapplicable data (?). Hosts with more than one species of parasite were considered as independent entities to allow the recognition of the mechanisms responsible for these associations (Brooks & McLennan 1991, 1993; Boeger & Kritsky 1997). A host phylogeny was then reconstructed based solely on parasitological information and compared with the phylogenetic hypotheses based on host characters. The coded parasite cladogram was mapped onto the host cladogram to determine congruence.

## SYSTEMATICS

Subclass POLYONCHOINEA Bychowsky, 1937  
Order DACTYLOGYRIDEA Bychowsky, 1937  
Family DACTYLOGYRIDAE Bychowsky, 1933

### Genus *Rhinoxenus*

Kritsky, Boeger & Thatcher, 1988

TYPE SPECIES. — *Rhinoxenus piranhus* Kritsky, Boeger & Thatcher, 1988, from *Pygocentrus nattereri* Kner, 1858 (Characidae).

OTHER SPECIES INCLUDED. — *Rhinoxenus arietinus* Kritsky, Boeger & Thatcher, 1988 from *Leporinus agassizii* Steindachner, 1876, *L. elongatus* Valenciennes, 1849, *L. friderici friderici* (Bloch, 1794), *L. lacustris* Amaral Campos, 1945, *L. obtusidens* (Valenciennes, 1836), *Schizodon altoparanae* Garavello & Britski, 1990, *S. borellii* (Boulenger, 1990), *S. fasciatus* Spix & Agassiz, 1829, *Schizodon* sp. and *Rhytioidus argenteofuscus* Kner, 1858 (Anostomidae); *R. bulbosus* Valenciennes, 1836 and *S. spilopleura* Kner, 1858 (Characidae); *R. anacaudiae* n. sp., from *Triportheus* cf. *nematurus*, *Triportheus* sp. and *Brycon* sp. (Characidae); *R. curimbatae* n. sp., from *Prochilodus* cf. *lineatus* (Prochilodontidae); *R. euryxenus* n. sp. from *Serrasalmus gouldingi* Fink & Machado Allison, 1992, *S. marginatus*, *S. rhombeus* (Linnaeus, 1766), *S. spilopleura*, *S. striolatus* Steindachner, 1908 (Characidae), *Leporinus agassizii* (Anostomidae); *R. guianensis* n. sp., from *Curimata cyprinoides* (Linnaeus, 1766) (Curimatidae); and several undeterminate *Rhinoxenus* species from *Hydrolicus scomberoides* (Cuvier, 1816) (Cynodontidae).

EMENDED DIAGNOSIS. — Dactylogyridae. Body divided into cephalic region, trunk, haptor (peduncle absent). Tegument smooth. Cephalic lobes, head organs, cephalic glands present. Eyes four. Pharynx muscular, glandular; intestinal caeca two, confluent in posterior trunk, lacking diverticula. Gonads overlapping; testis dorsal to germarium. Common genital pore near bifurcation of intestinal caeca. Vas deferens looping left intestinal cecum; seminal vesicle a dilation of vas deferens. Copulatory complex comprising a sclerotized male copulatory organ (MCO), accessory piece; MCO a coiled tube with counterclockwise rings (Kritsky *et al.* 1985, 1988), with conical base surrounded by two circular sclerotized tandem brims; proximal brim articulated to copulatory ligament of accessory piece. Copulatory ligament lying within rings of MCO; distal portion of the accessory piece expanded. Vagina sclerotized, sinistral, proximal portion of vagina with one or more loops. Seminal receptacle present. Vitellaria follicular. Haptor with 14 hooks, having ancyrocephaline distribution (Mizelle 1936); hook comprising shank of two subunits; pair of ventral anchors, a pair of spike-like dorsal anchors; ventral bar; dorsal bar absent. Parasites of the nasal cavity of the Neotropical characiform fishes.

#### REMARKS

The general features of the internal morphology of *Rhinoxenus* species are well documented by Kritsky *et al.* (1988) and Boeger *et al.* (1995).

Diagnostic features of the genus include: 1) presence of dorsal anchor modified into a spike-like sclerite; 2) absence of dorsal bar; 3) presence of hook from pair 2 located in two bilateral lobes of the trunk; and 4) two circular sclerotized tandem brims on the base of the MCO. The original diagnosis of *Rhinoxenus* does not include the two circular tandem sclerotized brims associated with the base of the MCO. These structures have been reported in species of *Dawestrema* (Kritsky *et al.* 1985) and of *Cacatuocotyle* (Boeger *et al.* 1997) but probably represent independent evolutionary events. Thus, the presence of these brims is considered a synapomorphy for *Rhinoxenus*. Kritsky *et al.* (1988) report that species of *Rhinoxenus* present all hooks with shank inflated proximally. *Rhinoxenus curimbatae* n. sp. is the only species of the genus that does not present this character. However, the absence of the shank inflation seems to be a second autapomorphic loss.

#### *Rhinoxenus piranhus*

Kritsky, Boeger & Thatcher, 1988

(Fig. 1A, B)

*Rhinoxenus piranhus* Kritsky, Boeger & Thatcher, 1988: 88, 89, figs 1-8.

TYPE HOST AND LOCALITY. — Nasal cavities of *Pygocentrus nattereri* (Characidae): Ilha Marchantaria, Rio Solimões, near Manaus, Amazonas, Brazil, 21.IX.1983, 15.VIII.1984, 14.IX.1985, 25-26.XI.1984.

MATERIAL EXAMINED. — **Brazil.** Rio Capucapu, Cachoeira das Garças, near Manaus, Amazonas, from *Pristobrycon* sp. (Characidae), 1.XI.1989, voucher specimens (INPA 446). — Rio Paraná, near Porto Rico, Paraná, from *Serrasalmus marginatus* (Characidae), 1992, voucher specimens (INPA 445); same locality, from *Serrasalmus spilopleura* (Characidae), 1992, voucher specimens (INPA 444). — Rio Uatumã, Lago Tapana, Santa Anna, Amazonas, from *Serrasalmus spilopleura* (Characidae), 2-3.XI.1989, voucher specimens (INPA 441 a-f; MNHN 173 HG-T1 216-216 bis; USNPC 95241).

**French Guiana.** Lagoa Manga, Igarapé Tapardou, from *Pygocentrus nattereri* (Characidae), 15-16.X.1996, voucher specimens (INPA 442 a-b; MNHN 174 HG-T1 217; USNPC 95242); same locality, from *Serrasalmus spilopleura* (Characidae), 15-16.X.1996, voucher specimens (INPA 443; MNHN 175 HG-T1 217 bis).

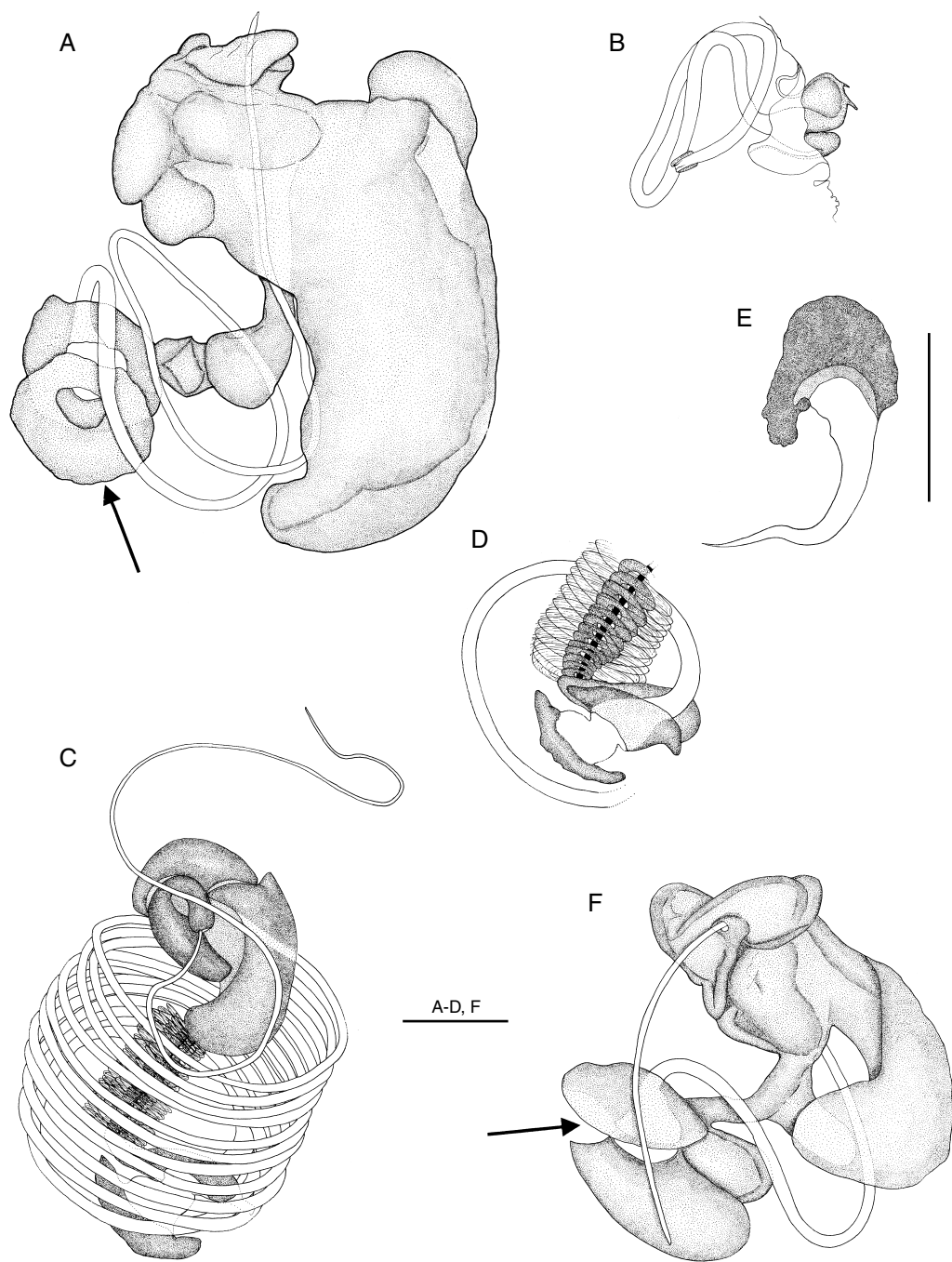


FIG. 1. — Sclerotized structures of selected *Rhinoxenus* species; **A**, *R. piranhus* Kritsky, Boeger & Thatcher, 1988, male copulatory organ (MCO); **B**, *R. piranhus*, vagina; **C**, *R. nyttus* Kritsky, Boeger & Thatcher, 1988, MCO; **D**, *R. nyttus*, detail of the base of the MCO (distal portion of MCO not shown); **E**, *R. nyttus*, ventral anchor; **F**, *R. arietinus* Kritsky, Boeger & Thatcher, 1988, MCO. Arrow indicates the circular tandem sclerotized brims. Scale bars: A-D, F, 20  $\mu$ m; E, 50  $\mu$ m.

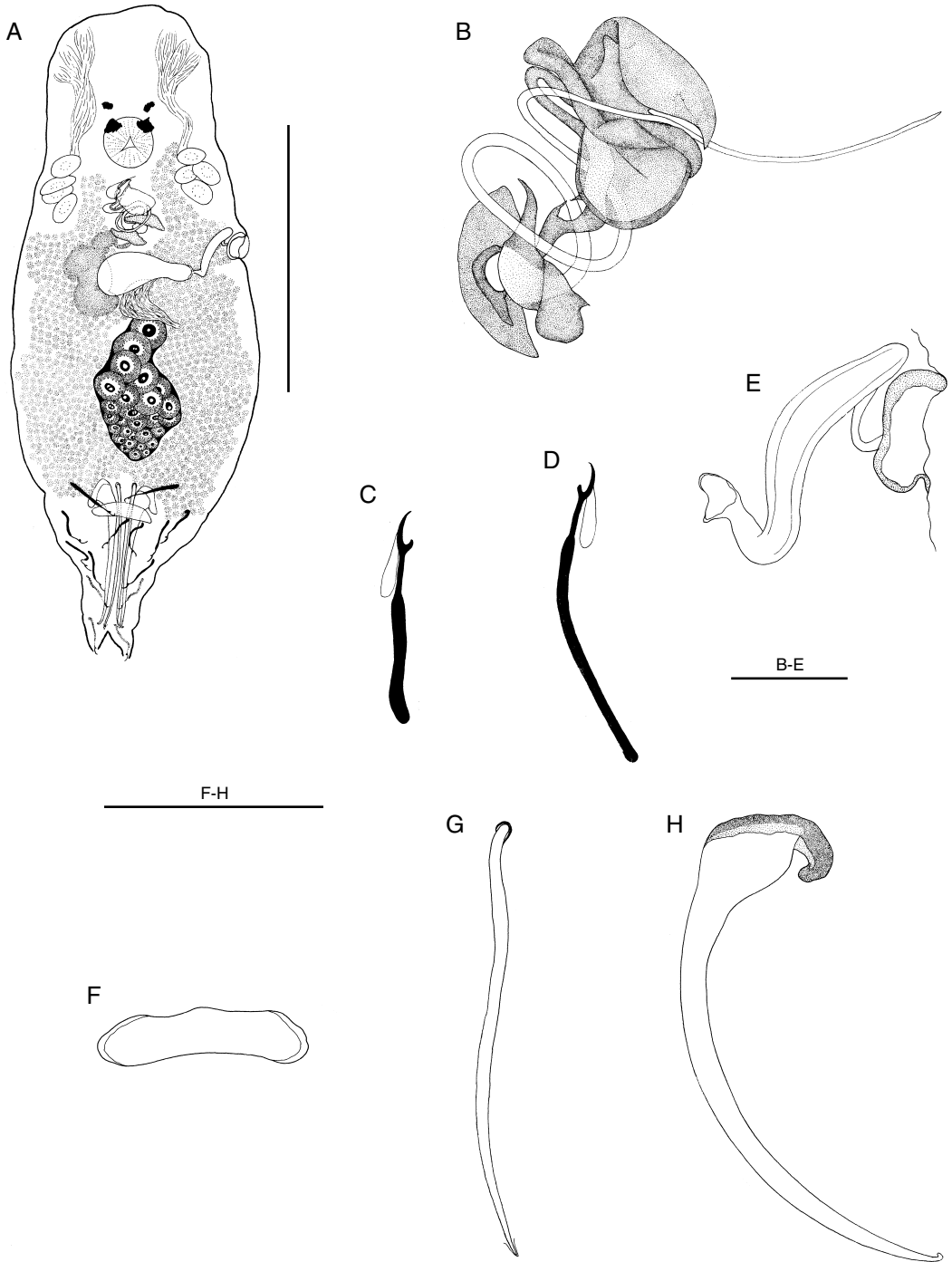


FIG. 2. — *Rhinoxenus anaclaudiae* n. sp.; **A**, holotype (ventral); **B**, male copulatory organ (MCO); **C**, hook from pair 2; **D**, hook from pairs 1, 3-7; **E**, vagina; **F**, ventral bar; **G**, dorsal anchor; **H**, ventral anchor. Scale bars: A, 100  $\mu$ m; B-E, 10  $\mu$ m; F-H, 30  $\mu$ m.

TABLE 1. — Comparative measurements (in  $\mu\text{m}$ ) of sclerotized structures of specimens of *Rhinoxenus piranhus* Kritsky, Boeger & Thatcher, 1988 from *Serrasalmus spilopleura* from three localities of South America. Abbreviations: **AM**, Amazonas; **FG**, French Guiana; **PA**, Paraná.

	<i>Serrasalmus spilopleura</i> (AM)	N	<i>Serrasalmus spilopelura</i> (PA)	N	<i>Serrasalmus spilopleura</i> (FG)	N
<b>Copulatory organ</b>						
Ring diameter	31 (25-35)	16	—	—	24 (24-25)	2
<b>Ventral anchor</b>						
Length	128 (118-156)	16	136	1	159	1
Base width	36 (31-47)	16	45	1	36 (33-39)	2
<b>Dorsal anchor</b>						
Length	107 (96-123)	16	—	—	118	1
Base width	4 (3-5)	16	4	1	4 (3-4)	2
<b>Bar length</b>						
Ventral	60 (55-65)	16	63	1	59 (58-60)	2
<b>Hook lengths</b>						
Pair 1	19	1	—	—	—	—
Pair 2	24 (20-29)	10	24	1	—	—
Pair 3	28 (27-29)	3	35	1	—	—
Pair 4	27	1	33	1	32	1
Pair 5	25 (21-29)	4	28	1	—	—
Pair 6	31 (28-35)	2	—	—	—	—
Pair 7	—	—	—	—	—	—

TABLE 2. — Comparative measurements (in  $\mu\text{m}$ ) of sclerotized structures of specimens of *Rhinoxenus piranhus* Kritsky, Boeger & Thatcher, 1988 from four species of serrasalmin hosts. \*, *Serrasalmus spilopleura* from Amazonas, Paraná and French Guiana.

	<i>Pristobriccon</i> sp.	N	<i>Pygocentrus</i> <i>nattereri</i>	N	<i>Serrasalmus</i> <i>marginatus</i>	N	* <i>Serrasalmus</i> <i>spilopleura</i>	N
<b>Copulatory organ</b>								
Ring diameter	29	1	36	1	31	1	30 (24-35)	16
<b>Ventral anchor</b>								
Length	146	4	161	1	161	1	130 (118-159)	18
Base width	45	2	55	1	37	1	37 (31-47)	18
<b>Dorsal anchor</b>								
Length	118	5	131	1	105	1	107 (96-123)	19
Base width	4	1	5	1	4	1	4 (3-5)	17
<b>Bar length</b>								
Ventral	76	1	—	—	65	1	60 (55-65)	19
<b>Hook lengths</b>								
Pair 1	—	—	—	—	—	—	19	1
Pair 2	25	1	28	1	23	1	24 (20-29)	11
Pair 3	—	2	—	—	—	—	30 (27-35)	4
Pair 4	—	2	—	—	29	1	30 (27-28)	2
Pair 5	30	—	—	—	26	1	25 (21-29)	5
Pair 6	30	1	35	1	—	—	31 (28-35)	2
Pair 7	—	1	35	1	34	1	—	—

PREVIOUS RECORD. — Furo do Catalão, near Manaus Amazonas, Brazil from *Pygocentrus nattereri* (Characidae), 27.XI.1984.

COMPARATIVE MEASUREMENTS. — See Tables 1 and 2.

#### REMARKS

*Rhinoxenus piranhus* was adequately described as the type species of the genus by Kritsky *et al.* (1988). However, the MCO and the vaginal vestibule were redrawn for comparative purposes.

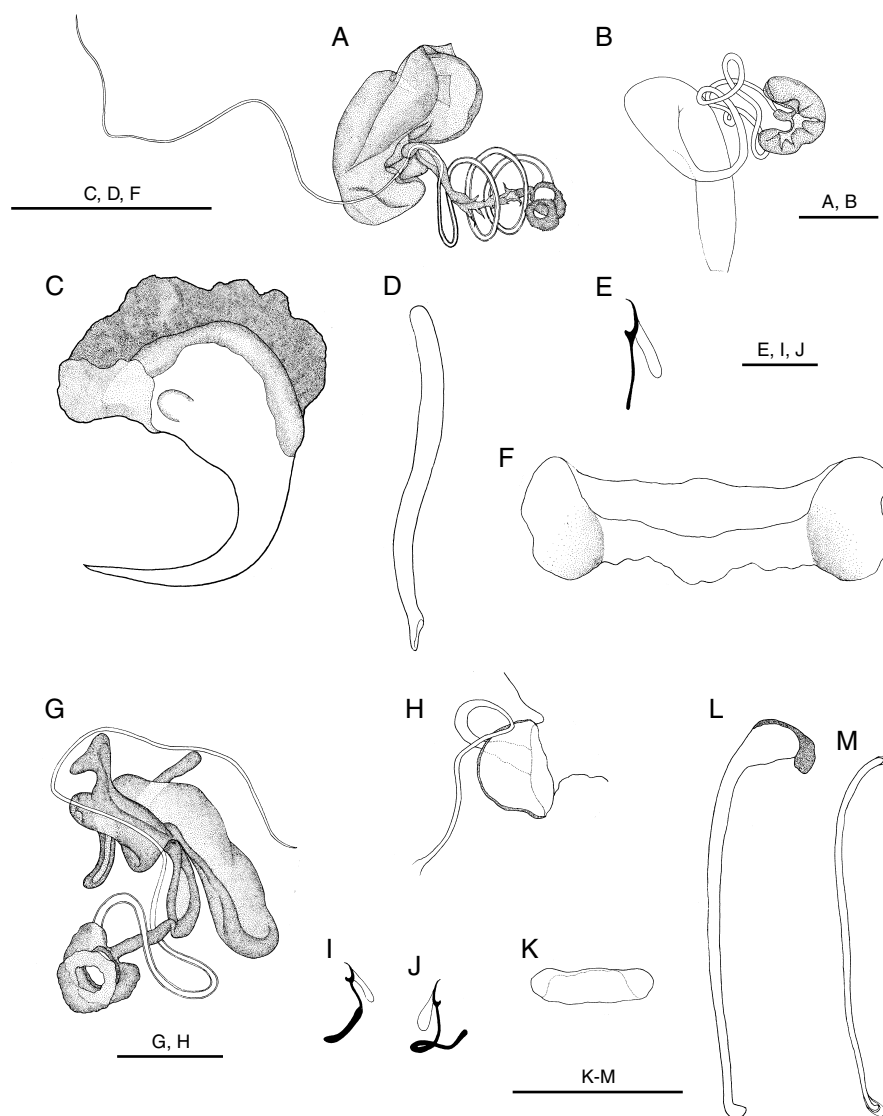


FIG. 3. — Sclerotized structures in *Rhinoxenus*; **A-F**, *R. curimbatae* n. sp.; **A**, male copulatory organ (MCO); **B**, vagina; **C**, ventral anchor; **D**, dorsal anchor; **E**, hook; **F**, ventral bar; **G-M**, *R. guianensis* n. sp.; **G**, male copulatory organ (MCO); **H**, vagina; **I**, hook from pair 2; **J**, hook from pairs 1, 3-7; **K**, ventral bar; **L**, ventral anchor; **M**, dorsal anchor. Scale bars: A, B, 20 µm; C, D, F, 30 µm; E, I, J, 15 µm; G, H, 10 µm; K-M, 50 µm.

*Rhinoxenus arietinus*  
Kritsky, Boeger & Thatcher, 1988  
(Fig. 1F)

*Rhinoxenus arietinus* Kritsky, Boeger & Thatcher, 1988: 88-92, figs 9-17.

TYPE HOST AND LOCALITY. — Nasal cavity of *Schizodon fasciatus* (Anostomidae), Ilha Marchantaria, Rio Solimões, near Manaus, Amazonas, Brazil, 25.XI.1983 (Kritsky *et al.* 1988).

MATERIAL EXAMINED. — **Brazil**. Rio Capucapu, Cachoeira das Garças, Manaus, Amazonas, from *Leporinus agassizii* (Anostomidae), 30.X.1989, voucher



TABLE 3. — Comparative measurements (in  $\mu\text{m}$ ) of sclerotized structures of specimens of *Rhinoxenus arietinus* Kritsky, Boeger & Thatcher, 1988 from *Leporinus elongatus* and *L. obtusidens* in two localities at Paraná State, Brazil. Abbreviations: **PA**, Rio Paraná; **TI**, Rio Tibagi.

	<i>Leporinus elongatus</i> (PA)	N	<i>Leporinus obtusidens</i> (PA)	N	<i>Leporinus elongatus</i> (TI)	N	<i>Leporinus obtusidens</i> (TI)	N
<b>Copulatory organ</b>								
Ring diameter	36 (32-40)	5	32 (28-39)	12	30 (27-35)	9	30	1
<b>Ventral anchor</b>								
Length	138 (138-149)	4	140 (129-164)	12	127 (108-136)	9	102	1
Base width	73 (68-78)	2	70 (63-75)	7	69 (65-73)	5	57	1
<b>Dorsal anchor</b>								
Length	154 (146-171)	5	157 (139-174)	12	147 (126-164)	8	23	1
Base width	17	1	17	2	—	—	14	1
<b>Bar length</b>								
Ventral	66	1	54 (50-60)	7	55 (50-60)	—	140	1
<b>Hook lengths</b>								
Pair 1	—	—	—	—	—	—	33	1
Pair 2	36	1	40 (35-47)	7	38 (33-42)	1	36	1
Pair 3	—	2	48-49	2	—	—	45	1
Pair 4	42	2	42 (38-45)	2	—	—	44	1
Pair 5	—	—	—	—	—	—	44	1
Pair 6	46	1	47	1	—	—	43	1
Pair 7	48	1	48	1	—	—	43	1

specimens (CHIOC 36282 a-b). — Rio Paraná, Porto Rico, Paraná, from *Leporinus elongatus* (Anostomidae), 1992, voucher specimens (CHIOC 36283 a-b; INPA 429; MNHN HG-T1 205-205 bis); same locality, from *Leporinus obtusidens* (Anostomidae), 1992, voucher specimens (INPA 428 a-c; MNHN HG-T1 204-240 bis; USNPC 95231). — Rio Paraná, Ressaco do pau velho, Porto Rico, Paraná, from *Leporinus elongatus* (Anostomidae), 1992, voucher specimens (INPA 430 a-c); from *Leporinus elongatus* (Anostomidae), 17.VI.1996, voucher specimens (USNPC 95232). — Rio Tibagi, near Jataizinho, Paraná, from *Leporinus elongatus* (Anostomidae), 28-29.V.1997, voucher specimens (CHIOC 35284 a-c; INPA 431 a-c; USNPC 95233); same locality, from *Leporinus obtusidens*, 28-29.V.1997, voucher specimens (CHIOC 36307 a-d; MNHN 164 HG-T1 206-206 bis). — Reservatório de Itaipu, Foz do Iguassu, Paraná, from *Leporinus friderici* (Anostomidae), 15.XI.1996, voucher specimens (CHIOC 36286 a-b; INPA 432; USNPC 95234); same locality, from *Schizodon* sp. (Anostomidae), 15.XI.1996, voucher specimens (CHIOC 36291 a-c; INPA 426 a-b; MNHN 161 HG-T1 203-203 bis; USNPC 95229). — Rio Paraná, near Porto Rico, Paraná, from *Leporinus friderici friderici* (Anostomidae), 1993, voucher specimens (CHIOC 36285 a-b; MNHN 165 HG-T1 207); same locality, from *Leporinus lacustris* (Anostomidae), 1993, voucher specimens (CHIOC 36287 a-b; INPA 427; USNPC 95230); same locality, from *Schizodon altoparanae* (Anostomidae), 1993, voucher specimens

(CHIOC 36288 a-c; INPA 424 a-b; MNHN 158 HG-T1 201-201 bis; USNPC 95227); same locality, from *Schizodon borelli* (Anostomidae), 1992, voucher specimens (CHIOC 36289 a-b; INPA 422; USNPC 95224-95226); same locality, from *Schizodon borelli* (Anostomidae), 1993, voucher specimens (CHIOC 36290 a-c; INPA 423 a-c; MNHN 156 HG-T1 198 bis-199-199 bis, 157 HG-T1 200-200 bis); same locality, from *S. knerii* (Steindachner, 1875) (Anostomidae), 1993, voucher specimens (USNPC 95228).

PREVIOUS RECORD. — Aquarium INPA, Manaus, Amazonas, Brazil from *Rhytioidus argenteofuscus* (Anostomidae), 8.II.1984 (Kritsky *et al.* 1988).

COMPARATIVE MEASUREMENTS. — See Tables 3 and 4.

#### REMARKS

*Rhinoxenus arietinus* is known from nine species of *Leporinus*, *Schizodon*, and *Rhytioidus*. *Leporinus elongatus* and *L. obtusidens* are reported as hosts in two different localities (both in the Rio Paraná and Rio Tibagi, PR, Brazil). Kritsky *et al.* (1988) considered the occurrence of *Rhinoxenus arietinus* in *Rhytioidus argenteofuscus* as accidental. However, this parasite occurs in other anostomids, and thus, it seems to represent a parasite specific to this family.

TABLE 4. — Comparative measurements (in  $\mu\text{m}$ ) of sclerotized structures of specimens of *Rhinoxenus arietinus* Kritsky, Boeger & Thatcher, 1988 of eight anostomid hosts. \*, *Leporinus elongatus* from Rio Paraná and Rio Tibagi; \*\*, *L. obtusidens* from Rio Paraná and Rio Tibagi.

	<i>Leporinus agassizii</i>	N	* <i>Leporinus elongatus</i>	N	<i>Leporinus friderici</i>	N	<i>Leporinus lacustris</i>	N
<b>Copulatory organ</b>								
Ring diameter	27 (21-33)	2	32 (27-40)	14	32 (30-35)	3	29 (27-30)	3
<b>Ventral anchor</b>								
Length	127 (99-156)	2	131 (108-149)	13	133 (118-14)	4	111 (106-113)	4
Base width	63 (53-73)	2	70 (65-78)	7	58 (52-67)	3	49 (40-54)	4
<b>Dorsal anchor</b>								
Length	130 (106-154)	2	150 (126-171)	13	146 (116-159)	4	115 (120-131)	3
Base width	12 (10-15)	1	17	1	15 (12-19)	4	14 (12-16)	4
<b>Bar length</b>								
Ventral	63	1	60 (50-66)	7	58	5	50	1
<b>Hook lengths</b>								
Pair 1	—	—	—	—	36	1	—	—
Pair 2	29	1	38 (33-42)	8	41 (36-45)	2	35 (34-38)	3
Pair 3	—	—	—	—	40	1	—	—
Pair 4	—	—	42	1	48 (47-49)	2	39 (38-40)	2
Pair 5	—	—	—	—	—	—	—	—
Pair 6	—	—	46	1	—	—	—	—
Pair 7	—	—	45	1	—	—	—	—
	** <i>Leporinus obtusidens</i>	N	<i>Schizodon altoparanae</i>	N	<i>Schizodon borelli</i>	N	<i>Schizodon sp.</i>	N
<b>Copulatory organ</b>								
Ring diameter	32 (28-39)	13	31 (30-33)	9	31 (27-35)	11	26-27	2
<b>Ventral anchor</b>								
Length	137 (102-164)	13	140 (134-154)	12	129 (121-144)	12	141 (134-147)	3
Base width	68 (57-75)	8	66 (63-71)	7	72 (66-80)	12	65 (55-75)	2
<b>Dorsal anchor</b>								
Length	154 (123-174)	13	172 (164-186)	12	130 (113-141)	14	143 (134-159)	3
Base width	16 (14-16)	3	20 (19-24)	6	19 (15-21)	4	—	—
<b>Bar length</b>								
Ventral	51 (40-60)	8	62 (58-65)	8	54 (50-58)	2	63	1
<b>Hook lengths</b>								
Pair 1	33	1	—	—	—	—	—	—
Pair 2	40 (35-47)	8	37	—	40 (37-44)	5	—	—
Pair 3	47 (45-49)	3	—	—	50	1	—	—
Pair 4	42 (38-45)	3	—	—	47	2	—	—
Pair 5	44	1	—	—	43	1	—	—
Pair 6	47 (43-47)	2	—	—	—	—	—	—
Pair 7	48 (43-48)	2	—	—	55	1	47	—

The specimens analyzed herein do not differ significantly from those described by Kritsky *et al.* (1988). However, the proximal projection of the accessory piece, that surrounds the first ring of the MCO (Kritsky *et al.* 1988: figs 11, 12), was not observed herein, and the two tandem brims associated to the base of the MCO (Fig. 1F) were not described by Kritsky *et al.*

(1988). The measurements of the sclerotized structures of the present material do not differ from those presented in the original description. *Rhinoxenus arietinus* differs from the other species of the genus by possessing two posterior muscular lobes on the haptor and a ventral anchor with a conspicuous superficial and deep root.

TABLE 5. — Comparative measurements (in  $\mu\text{m}$ ) of sclerotized structures of specimens of *Rhinoxenus nyttus* Kritsky, Boeger & Thatcher, 1988 from *Leporinus agassizii* and *Schizodon* sp.

	<i>Leporinus agassizii</i>	N	<i>Schizodon</i> sp.	N
<b>Copulatory organ</b>				
Ring diameter	31	1	27 (23-30)	3
<b>Ventral anchor</b>				
Length	90	1	73 (69-85)	6
Base width	45	1	36 (31-43)	6
<b>Dorsal anchor</b>				
Length	63	1	55 (51-59)	5
Base width	3	1	3 (2-3)	6
<b>Bar length</b>				
Ventral	62	1	45 (42-50)	7
<b>Hook lengths</b>				
Pair 1	15	1	18 (15-21)	4
Pair 2	20	1	18 (17-22)	6
Pair 3	25	1	23 (21-25)	5
Pair 4	27	1	23 (21-25)	4
Pair 5	19	1	18 (17-20)	18
Pair 6	21	1	22 (19-24)	3
Pair 7	26	1	21 (17-23)	3

*Rhinoxenus bulbovaginatus*

Boeger, Domingues &amp; Pavanelli, 1995

*Rhinoxenus bulbovaginatus* Boeger, Domingues & Pavanelli, 1995: 696-698, figs 1-8.

HOST AND LOCALITY. — Nasal cavities of *Salminus brasiliensis* (Characidae), Rio Paraná, near Porto Rico, Paraná, Brazil.

MATERIAL EXAMINED. — **Brazil.** Rio Miranda, Passo do Lontra, Mato Grosso do Sul, from *Salminus brasiliensis* (Characidae), 5.VIII.1998, voucher specimens (INPA 421 a-c; MNHN 155 HG-T1 197-197 bis-198; MZUSP 5934 a-b; USNPC 95223).

MEASUREMENTS. — Copulatory organ ring diameter 27 (21-37; n = 5); ventral anchor 121 (117-122; n = 5) long, 32 (30-32; n = 5) wide; dorsal anchor 129 (125-132; n = 5) long; 5 (n = 5) wide; ventral bar 64 (60-67; n = 5) long; 12 (n = 5) wide; hook pair 1 37 (36-38; n = 2); hook pair 2 33 (30-35; n = 4); hook pair 3 48; hook pair 4 52; hook pair 5 45; hook pair 6 51; hook pair 7 49 (47-52; n = 3).

## REMARKS

*Rhinoxenus bulbovaginatus* is characterized by possessing the point of the ventral anchor in the shape of a "fish-hook"; posterolateral expansions in the ventral bar for articulation to the ventral anchor; and vagina sclerotized with cup-shape vestibule.

*Rhinoxenus nyttus*

Kritsky, Boeger &amp; Thatcher, 1988

(Fig. 1C-E)

*Rhinoxenus nyttus* Kritsky, Boeger & Thatcher, 1988: 92, 93, figs 18-24.

TYPE HOST AND LOCALITY. — Nasal cavities of *Schizodon fasciatus* (Anostomidae), Ilha Marchantaria, Rio Solimões, near Manaus, Amazonas, Brazil, 25.XI.1983.

MATERIAL EXAMINED. — **Brazil.** Usina Hidrelétrica de ITAIPU, Foz do Iguassu, Paraná, from *Schizodon* sp. (Anostomidae), 15.X.1996, voucher specimens (CHIOC 36292 a-c; INPA 433; MNHN 167 HG-T1 208-208 bis; USNPC 95235). — Rio Capucapu, Cachoeira das Garças, near Manaus, Amazonas, from *Leporinus agassizii* (Anostomidae), 30.X.1989, voucher specimens (INPA 434; USNPC 95236).

COMPARATIVE MEASUREMENTS. — See Table 5.

## REMARKS

*Rhinoxenus nyttus* is apparently restricted to members of Anostomidae. The specimens analyzed here are similar to those described by Kritsky *et al.* (1988), except by the possession of a more extensive sclerotized cap on the root ventral anchor (Fig. 1E). The original description does not mention the presence of the brims of the MCO, observed in all studied specimens (Fig. 1C, D).

TABLE 6. — Comparative measurements (in  $\mu\text{m}$ ) of sclerotized structures of specimens of *Rhinoxenus anaclaudiae* n. sp. from *Triporthus* cf. *nematurus*, *Triporthus* sp., and *Brycon* sp.

	<i>Triporthus</i> cf. <i>nematurus</i>	N	<i>Triporthus</i> sp.	N	<i>Brycon</i> sp.	N
<b>Copulatory organ</b>						
Ring diameter	22 (18-26)	23	18 (14-20)	9	13	1
<b>Ventral anchor</b>						
Length	74 (67-85)	22	73 (67-84)	9	87	1
Base width	20 (17-23)	20	22 (18-26)	9	21	1
<b>Dorsal anchor</b>						
Length	65 (56-72)	17	67 (62-73)	8	68	1
Base width	2 (2-3)	23	2 (2-3)	9	3	1
<b>Bar length</b>						
Ventral	33 (30-36)	16	31 (30-33)	8	30	1
<b>Hook lengths</b>						
Pair 1	—	—	—	—	—	—
Pair 2	21 (19-24)	5	21 (20-22)	3	—	—
Pair 3	14	3	—	—	—	—
Pair 4	—	—	—	—	—	—
Pair 5	—	—	—	—	—	—
Pair 6	—	—	—	—	—	—
Pair 7	—	—	—	—	—	—

Parasites of each host species present little variation in size in almost all the analyzed structures.

*Rhinoxenus nyttus* is characterized by possessing a ventral bar with lateral projections that serve as articulation to the ventral anchor; long chaliceshaped vaginal vestibule; and ventral anchor with wavy point, representing 1/3 of the total length of the anchor.

*Rhinoxenus anaclaudiae* n. sp.  
(Fig. 2)

TYPE MATERIAL. — Holotype (CHIOC 36300); 23 paratypes (CHIOC 36301 a-e; INPA 439 a-g; MNHN 171 HG-T1 212-212 bis-213; MZUSP 5933 a-h; USNPC 95239).

ETYMOLOGY. — The species is named after Dr Ana Claudia dos Santos Brasil, a specialist of Polychaeta.

TYPE HOST AND LOCALITY. — Nasal cavities of *Triporthus* cf. *nematurus* (Characidae), Rio Miranda, Passo do Lontra, Mato Grosso do Sul, Brazil, 30.XI.1996.

OTHER MATERIAL EXAMINED. — **Brazil.** Rio Miranda, Passo do Lontra, Mato Grosso do Sul, from *Brycon* sp. (Characidae), 5.VIII.1998, voucher specimens (CHIOC 36302). — Baía da Medalha, Rio Miranda, Mato Grosso do Sul, from *Triporthus* sp. (Characidae), 4.VIII.1998, voucher specimens (INPA 440

a-d; MNHN 172 HG-T1 214-214 bis-215; USNPC 95240).

COMPARATIVE MEASUREMENTS. — See Table 6.

DESCRIPTION

Body pyriform, 254 (n = 1) long; greatest width 98 (n = 1) at body midlength. Cephalic lobes poorly developed; three pairs of cephalic organs; cephalic glands posterolateral to pharynx. Members of posterior pair of eyes larger, closer than those of anterior pair; eye granules elongate. Pharynx 19 (18-20; n = 5) in diameter. Haptor subtriangular, 71 (n = 1) long, 57 (n = 1) wide. Ventral anchor with inconspicuous roots, sclerotized cap of base with projection for articulation to ventral bar, shaft evenly curved, point short, strongly recurved. Dorsal anchor with blunt proximal end, pointed distal end, terminations with conspicuous sclerotized caps. Ventral bar flattened, with slightly thickened ends. Hook pair 2 with erect thumb, lightly curved shaft, short point, proximal 3/4 of shank inflated; filamentous hook (FH) loop extended to near beginning of shank dilation; remaining hooks with erect thumb, long shaft, lightly curved, shank inflated proximally; FH loop extended to near beginning of shank dilation. Male copulatory

organ a coiled tube with approximately two rings. Testis oval, 54 (43-64;  $n = 2$ ) long, 24 ( $n = 1$ ) wide; seminal vesicle fusiform. Germarium 49 (42-54;  $n = 4$ ) long, 29 (26-34;  $n = 4$ ) wide. Ootype, uterus not observed. Vagina sclerotized, proximally wide, tapering distally, distal loop; vaginal vestibule sclerotized, cup shaped. Seminal receptacle pyriform. Large dorsal prostate. Vitellaria coextensive with cecae; vitelline commissure anterior to germarium. Egg not observed.

#### REMARKS

*Rhinoxenus anaclaudiae* n. sp. differs from its congeners in possessing a ventral anchor with evenly curved and short shaft and strongly recurved point. *Rhinoxenus anaclaudiae* n. sp. is apparently restricted to members of Characoidea (*sensu* Buckup 1998).

#### *Rhinoxenus curimbatae* n. sp. (Fig. 3A-F)

TYPE MATERIAL. — Holotype (CHIOC 36303); paratypes (CHIOC 36304 a-b; INPA 419; MNHN 153 HG-T1 195).

ETYMOLOGY. — The specific epithet refers to the local name of the host, "curimbata".

TYPE HOST AND LOCALITY. — Nasal cavities of *Prochilodus* cf. *lineatus* (Prochilodonidae), Represa Capivari-Cachoeira, Municipality of Campina Grande do Sul, metropolitan area of Curitiba, Paraná, Brazil, 15.III.1995.

#### DESCRIPTION

Body 700 ( $n = 1$ ) long; greatest width 130 ( $n = 1$ ) at body midlength. Eyes usually present, equidistant; eye granules elongate. Pharynx spherical, 30 ( $n = 1$ ) in diameter. Haptor subtrapezoidal, 82 ( $n = 1$ ) long, 75 ( $n = 1$ ) wide. Ventral anchor 50 (42-56;  $n = 5$ ) long, base 42 (30-53;  $n = 4$ ) wide, superficial, roots inconspicuous, base with sclerotized cap articulated with ventral bar, knob-like projection on base, short recurved shaft, elongate straight point. Dorsal anchor 50 (31-59;  $n = 4$ ) long, base 4 (3-5;  $n = 4$ ) wide, robust, with blunt proximal end, straight shaft, distal end diagonally truncated. Ventral bar 42 (30-53;  $n = 1$ )

long with expanded ends. Hooks 14 (11-17;  $n = 15$ ) long, similar in shape, truncate thumb, evenly curved shaft, point, shank without inflation, FH loop extending to half of shank. Male copulatory organ a coiled tube with approximately 3.5 rings; greatest ring 27 (24-29;  $n = 4$ ) in diameter; copulatory ligament twisted. Gonads, ootype, uterus, seminal receptacle not observed. Vagina sclerotized; distal portion tubular, sinuous; proximal end wide; vaginal vestibule heavily sclerotized, cup-shaped. Egg not observed.

#### REMARKS

*Rhinoxenus curimbatae* n. sp. resembles *R. nyttus* based on the morphology of the MCO. However, it differs from this and other species of the genus by possessing dorsal anchors with distal end diagonally truncated, ventral anchors with short recurved shafts and elongate straight points, heavily sclerotized cup-shaped vaginal vestibule, and hooks with shanks not inflated.

#### *Rhinoxenus guianensis* n. sp. (Fig. 3G-M)

TYPE MATERIAL. — Holotype (CHIOC 36305); paratypes (CHIOC 36306 a-d; INPA 420; MNHN 154 HG-T1 196; USNPC 95222).

ETYMOLOGY. — The specific epithet refers to the type locality from which the species was collected.

TYPE HOST AND LOCALITY. — Nasal cavities of *Curimata cyprinoides* (Curimatidae), Iracoubo, Degrad Forian, French Guiana, 8-10.X.1996.

#### DESCRIPTION

Eyes usually present, equidistant, members of posterior pair closer than those of anterior pair; eyes granules elongate. Ventral anchor delicate, 115 (106-125;  $n = 5$ ) long, base 19 (15-22;  $n = 3$ ) wide, roots inconspicuous; base with sclerotized cap articulated to ventral bar; straight shaft, point short, truncated, golf-club shaped. Dorsal anchor delicate, slender, 98 (95-100;  $n = 5$ ) long; with blunt proximal, distal ends, slightly sinuous shaft; each end with conspicuous sclerotized cap. Ventral bar 35 (34-38;  $n = 5$ ) long. Hook pair 2 21 (20-23;  $n = 4$ ) long, erect thumb, shaft, point

evenly curved, proximal 2/3 of shank inflation; FH loop extending to near beginning of shank dilation. Hook pairs 1, 3-7 22 (20-24;  $n = 3$ ) long, elongate, erect thumb, lightly curved shaft, short point, proximal 2/3 of shank inflated; FH loop extending to near beginning of shank dilation. Male copulatory organ a coiled tube with approximately 1.5 rings, 15 (14-17;  $n = 4$ ) in diameter. Gonads, ootype, uterus, seminal receptacle not observed. Vagina sclerotized; with a subterminal loop, distally expanded; vestibule sclerotized, cup-shaped. Eggs not observed.

#### REMARKS

All specimens of *Rhinoxenus guianensis* n. sp. were mounted in Hoyer's medium. Measurements and description of internal organs, therefore, are limited. The new species differs from all other congeneric species by possessing ventral anchors with straight shafts, short, truncated, club-shaped points and dorsal anchors with distal portions truncated and curved.

#### *Rhinoxenus euryxenus* n. sp. (Fig. 4)

TYPE MATERIAL. — Holotype (CHIOC 36293); 7 paratypes (CHIOC 36294 a-g; INPA 435 a-c; MNHN 168 HG-T1 209-209 bis).

ETYMOLOGY. — The specific epithet is from Greek (*eury* = broad + *xen/o* = guest) and refers to the wide occurrence of this parasite within Serrasalminae.

TYPE HOST AND LOCALITY. — Nasal cavities of *Serrasalmus marginatus* (Characidae), Baía da Medalha, Rio Paraná, Matogrosso do Sul, Brazil, 18.VI.1996.

OTHER MATERIAL EXAMINED. — **Brazil.** Rio Uatumã, lago Tapanã, Santa Anna, Amazonas, from *Serrasalmus gouldingi* (Characidae), 2-3.XI.1989, voucher specimens (CHIOC 36297). — Rio Miranda, Passo do Lontra, Mato Grosso do Sul, from *Serrasalmus marginatus* (Characidae), 31.XI.1996, voucher specimens (CHIOC 36299). — Baía da Medalha, Rio Paraná, Matogrosso do Sul, from *Serrasalmus marginatus* (Characidae), 18-19.VI.1996, voucher specimens (INPA 436 a-b; MNHN 169 HG-T1 210-210 bis; USNPC 95237). — Rio Iatapu, lago Maracanã, Manaus, Amazonas, from *Serrasalmus rhombeus* (Characidae), 2.XI.1989, voucher specimens (CHIOC 36296; INPA 437 a-b; MNHN 170 HG-T1 211; USNPC 95238). — Rio Paraná, near Porto Rico,

Paraná, from *Serrasalmus spilopleura* (Characidae), 1992, voucher specimens (CHIOC 36298). — Rio Capucapu, near the confluence of the Rio Jatapu, Cachoeira das Garças, Amazonas, from *Serrasalmus striolatus* (Characidae), 31.XI.1989, voucher specimens (CHIOC 36295); same locality, from *Leporinus agassizii* (Anostomidae), 31.XI.1989, voucher specimens (INPA 438 a-b).

COMPARATIVE MEASUREMENTS. — See Tables 7 and 8.

#### DESCRIPTION

Body fusiform, 607 (480-720;  $n = 10$ ) long; greatest width 176 (150-210;  $n = 9$ ) at body midlength. Cephalic lobes poorly developed; three pairs of cephalic organs; cephalic glands posterolateral to pharynx. Eyes equidistant; members of anterior pair smaller than those of posterior pair; eye granules elongate. Pharynx spherical, 42 (35-54;  $n = 11$ ) in diameter. Haptor subtrapezoidal, 96 (64-115;  $n = 11$ ) long, 115 (86-140;  $n = 11$ ) wide. Ventral anchor with inconspicuous roots; base with sclerotized cap articulated with ventral bar; shaft recurved near midlength; point with saucer-like termination. Dorsal anchor with blunt proximal end covered by conspicuous sclerotized cap, straight shaft, tapered distal end. Ventral bar with expanded ends, irregularly sclerotized. Hook pair 2 robust, lying in small lobes on posterior trunk, with thumb erect, robust, shaft short, evenly short curved point; proximal 3/4 of shank inflated; FH loop extending to near beginning of shank dilation. Hooks pairs 1, 3-7 with erect thumb, delicate evenly curved shaft, short point; proximal 4/5 of shank long inflated; FH loop extending to near beginning of shank dilation. Male copulatory organ a coiled tube with approximately 1.5 to 2 rings; copulatory ligament twisted. Testis elongate, 120 ( $n = 1$ ) long, 25 ( $n = 1$ ) wide; seminal vesicle fusiform; prostate in two dorsolateral fields. Germarium elongate, 63 (56-70;  $n = 2$ ) long, 32 (29-37;  $n = 2$ ) wide. Ootype, uterus not observed. Vagina sclerotized, distal portion with loop; vestibule sclerotized, cup-shaped, often everted (Fig. 4B). Seminal receptacle elongate. Vitellaria coextensive with caecae; vitelline commissure anterior to germarium. Egg not observed.

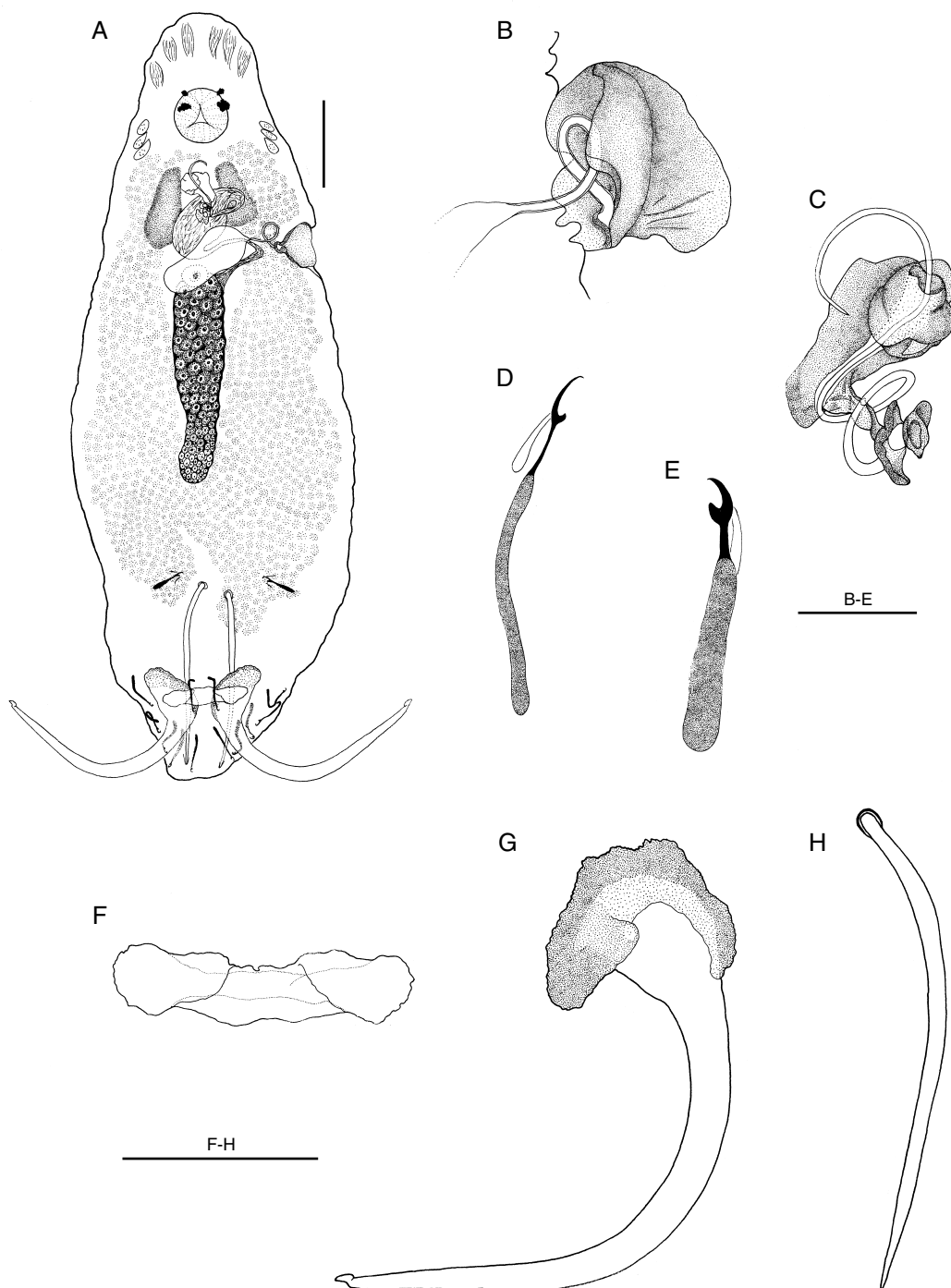


FIG. 4. — *Rhinoxenus euryxenus* n. sp.: **A**, holotype (ventral); **B**, vagina; **C**, male copulatory organ (MCO); **D**, hook from pairs 1, 3-7; **E**, hook from pair 2; **F**, ventral bar; **G**, ventral anchor; **H**, dorsal anchor. Scale bars: A, 100  $\mu$ m; B-E, 10  $\mu$ m; F-H, 50  $\mu$ m.

TABLE 7. — Comparative measurements (in  $\mu\text{m}$ ) of sclerotized structures of specimens of *Rhinoxenus euryxenus* n. sp. from *Serrasalmus marginatus* from two localities of Brazil. \*, Rio Paraná, Paraná; \*\*, Rio Miranda, Mato Grosso do Sul.

	<i>*Serrasalmus marginatus</i>	N	<i>**Serrasalmus marginatus</i>	N
<b>Copulatory organ</b>				
Ring diameter	33 (24-37)	23	29	1
<b>Ventral anchor</b>				
Length	152 (137-175)	24	144	1
Base width	55 (44-63)	22	49	1
<b>Dorsal anchor</b>				
Length	129 (123-151)	16	123	1
Base width	5 (4-6)	21	4	1
<b>Bar length</b>				
Ventral	82 (71-82)	15	77	1
<b>Hook lengths</b>				
Pair 1	25 (16-34)	2	—	—
Pair 2	29 (27-30)	8	26	1
Pair 3	40 (34-49)	6	—	—
Pair 4	37 (33-41)	6	—	—
Pair 5	33 (30-35)	3	—	—
Pair 6	34 (31-38)	3	—	—
Pair 7	36 (32-38)	3	—	—

TABLE 8. — Comparative measurements (in  $\mu\text{m}$ ) of sclerotized structures of specimens of *Rhinoxenus euryxenus* n. sp. from five serrasalmids and one anostomid hosts. \*, *Serrasalmus marginatus* from Rio Paraná and Rio Miranda.

	<i>Serrasalmus gouldini</i>	N	<i>*Serrasalmus marginatus</i>	N	<i>Serrasalmus rhombeus</i>	N	<i>Serrasalmus striolatus</i>	N	<i>Serrasalmus spilopleura</i>	N	<i>Leporinus agassizii</i>	N
<b>Copulatory organ</b>												
Ring diameter	—	—	33 (24-37)	24	37 (31-41)	3	37	1	34	1	32 (31-32)	2
<b>Ventral anchor</b>												
Length	142	1	153 (140-177)	25	150 (137-162)	3	124	1	150	1	147 (142-152)	2
Base width	49	1	55 (49-63)	22	49 (48-50)	3	33	1	62	1	42 (39-46)	2
<b>Dorsal anchor</b>												
Length	123	1	128 (123-151)	17	129 (121-133)	3	119	1	133	1	133 (129-137)	2
Base width	4	1	5 (4-6)	21	4 (4-5)	3	3	1	4	1	3 (3-4)	2
<b>Bar length</b>												
Ventral	77	1	83 (76-90)	22	72 (61-81)	4	57	1	92	1	55	1
<b>Hook lengths</b>												
Pair 1	—	—	25 (16-34)	2	21	1	—	—	—	—	28	1
Pair 2	29	1	29 (26-30)	9	27	2	27	1	39	1	26	1
Pair 3	—	—	40 (34-49)	6	—	—	—	—	—	—	29	1
Pair 4	—	—	37 (33-41)	6	28	1	—	—	—	—	28	1
Pair 5	—	—	33 (30-35)	3	32 (31-33)	2	—	—	34	1	—	—
Pair 6	—	—	34 (31-38)	4	—	—	—	—	—	—	—	—
Pair 7	36	1	36 (32-38)	3	30	2	—	—	—	—	34	1

## REMARKS

*Rhinoxenus euryxenus* n. sp. closely resembles *R. piranhus* based on the morphology of MCO and point of the ventral anchor. The new species, however, differs from *R. piranhus* by possessing ventral anchors with shafts strongly recurved near midlength (relatively straight shaft in *R. piranhus*)

and lacking the small terminal protuberances on the ventral bar as described by Kritsky *et al.* (1988: fig. 4) for *R. piranhus*. *Rhinoxenus euryxenus* n. sp. appears ubiquitous to fishes belonging to *Serrasalmus*. The occurrence of *R. euryxenus* n. sp. on *Leporinus agassizii* (Anostomidae) is considered accidental.



TABLE 9. — Matrix used in reconstruction of evolutionary relationship of *Rhinoxenus* species.

Taxon	Transformation series									
	A	B	C	D	E	F	G	H	I	J
Outgroup	0	0	0	0	0	0	0	0	0	0
<i>R. nyttus</i>	1	1	1	1	1	1	0	0	0	0
<i>R. curimbatae</i> n. sp.	1	1	1	1	0	0	2	0	0	?
<i>R. bulbovaginatus</i>	1	1	?	0	1	1	1	0	0	1
<i>R. arietinus</i>	1	1	1	1	0	1	0	1	1	1
<i>R. guianensis</i> n. sp.	1	1	1	0	1	1	2	1	1	?
<i>R. anacaudiae</i> n. sp.	1	1	1	0	0	1	2	1	1	?
<i>R. piranhus</i>	1	1	1	0	1	1	2	1	2	1
<i>R. euryxenus</i> n. sp.	1	1	1	0	1	1	2	1	2	1

TABLE 10. — Data matrix listing binary codes indicating phylogenetic relationships among eight species of *Rhinoxenus* and their hosts.

Hosts	Binary code													
<i>Acestrorhynchus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Anostomidae 1	1	0	0	0	0	0	0	0	1	0	0	0	0	1
Anostomidae 2	0	0	0	1	0	0	0	0	0	0	1	1	1	1
Chilodontidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Crenuchidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Curimatidae	0	0	0	0	1	0	0	0	0	0	1	1	1	1
Erythrinidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gasteropelecidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hemiodontidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Parodontidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Prochilodontidae	0	1	0	0	0	0	0	0	1	0	0	0	0	1
<i>Salminus</i>	0	0	1	0	0	0	0	0	0	0	0	0	1	1
Serrasalminae 1	0	0	0	0	0	0	1	0	0	1	1	1	1	1
Serrasalminae 2	0	0	0	0	0	0	0	1	0	1	1	1	1	1
<i>Triportheus</i>	0	0	0	0	0	1	0	0	0	0	1	1	1	1

## CHARACTER ANALYSIS

Numbers in parenthesis preceding the definition of a character refers to coding in the matrix: (0) represents the plesiomorphic state and (?) denotes missing or inapplicable data; numbers between square brackets refer to respective evolutionary changes depicted in cladogram (Fig. 5). The matrix of characters used for this analysis is presented in the Table 9. Transformation series 7 and 9 were considered ordered in the analysis.

**A. Dorsal bar.** (0) present; (1) absent [1].

**B. Shape of dorsal anchor.** (0) shaft and point clearly differentiated; (1) shaft and point not differentiated (Figs 2G; 3D, M; 4H) [2].

**C. Circular tandem sclerotized brims of Male copulatory organ (MCO).** (0) absent (Dominigues & Boeger 2002: fig. 2); (1) present [3].

**D. Shape of ventral anchor.** (0) anchor elongate, shaft longer than point (Figs 2H; 3L; 4G) [4]; (1) anchor short, shaft shorter than point (Figs 1E; 3C) [11, 18].

**E. Ventral bar.** (0) bar with extremities lightly expanded (Figs 2F; 3F; 4F) [5]; (1) bar with projections for articulation with ventral anchor (Kritsky *et al.* 1988: figs 4, 23) [12, 16, 21, 23].

**F. MCO.** (0) MCO with more than three rings from the base (Figs 1C; 3A) [6]; (1) MCO with less than three rings (Figs 1A, F; 2B; 3G; 4C) [14].

**G. Vaginal vestibule.** (0) absent (Kritsky *et al.* 1988: fig. 9) [19]; (1) vestibule chalice shaped, longer than wide (Kritsky *et al.* 1988: fig. 18) [7]; (2) vestibule cup shaped, vestibule wider than long (Figs 1B; 2E; 3B, H; 4B) [13, 20].

**H. Vagina.** (0) sinuous with more than one loop (Fig. 3B) [8]; (1) sinuous with only one loop (Figs 1B; 2E; 3H; 4B) [15].

**I. Point of ventral anchor.** (0) acute (Figs 1E; 3C) [9]; (1) blunt (Figs 2H; 3L) [17]; (2) flattened (Fig. 4G) [22].

**J. Hook pair 2.** (0) located within haptor; (1) located in two bilateral lobes in trunk (Kritsky *et al.* 1988: figs 1, 9, 18, 21; Boeger *et al.* 1995: fig. 1) [10].

The phylogenetic hypothesis of *Rhinoxenus* is based exclusively on sclerotized structures. The internal anatomy of *Rhinoxenus* species is redundant and, therefore, provides no evolutionary information. Similarly, morphology of the hooks does not vary for species of the genus and represents non-informative autapomorphies (e.g., hooks with shank not inflated in *Rhinoxenus curimbatae* n. sp.). The transformation series that describes the relative position of the eyes (transformation series 1 of Boeger *et al.* 1995) was not included in this study because it was not possible to define the state for some species.

## PHYLOGENY

The hypothesis of the sister-group relationship of the studied species, one of four equally parsimonious trees produced through the analysis (consistency index = 66%; retention index = 66%; length = 18), is presented in Figure 5. Monophyly of the genus is supported by three synapomorphies: 1) absence of dorsal bar; 2) dorsal anchor modified in probe form; and 3) presence of circular tandem sclerotized brims associated with the base of the MCO.

The previous hypothesis (Boeger *et al.* 1995) suggests that *R. arietinus* is sister group of (*R. nyttus* (*R. bulbovaginatus*, *R. piranhus*)). The present hypotheses, with the inclusion of four new taxa and new transformation series, disagrees significantly from that proposed by Boeger *et al.* (1995). *Rhinoxenus nyttus* + *R. curimbatae* n. sp. appear as sister group of the common ancestor of all other congeneric species. Boeger *et al.* (1995) suggest that *R. bulbovaginatus* is sister-group of

*R. piranhus*. However, in our hypotheses, *R. bulbovaginatus* is sister-group of (*R. arietinus* (*R. anacaudiae* n. sp., *R. guianensis* n. sp. (*R. piranhus*, *R. euryxenus* n. sp.))). The relationship of these five taxa is supported by one synapomorphy, with 100% of consistence: 1) point of ventral anchor not acute (blunt or flattened).

The sister relationships of *R. nyttus*, *R. curimbatae* n. sp., *R. bulbovaginatus* n. sp., and *R. arietinus* were identical in the four equally parsimonious trees. Consensus support existed for these relationships including the clade composed by *R. guianensis* n. sp. + *R. anacaudiae* n. sp. + *R. euryxenus* n. sp. + *R. piranhus*. Bootstrap support ( $\geq 50\%$ ) exists for the clade composed by *R. arietinus* + *R. guianensis* n. sp. + *R. anacaudiae* n. sp. + *R. euryxenus* n. sp. + *R. piranhus*, and the clade composed by *R. guianensis* n. sp. + *R. anacaudiae* n. sp. + *R. euryxenus* n. sp. + *R. piranhus*. The other three most parsimonious trees differ from that in Figure 5 primarily by the phylogenetic position of *R. guianensis* n. sp., *R. piranhus*, and *R. euryxenus* n. sp. The character "presence of ventral bar with articulation for ventral anchor" sometimes appears as a homoplasy for *R. guianensis* n. sp. and *R. piranhus*, sometimes as a synapomorphy uniting these two taxa. When the transformation series is removed from the analysis, the hypothesis presented in Figure 5 is the single most parsimonious cladogram produced.

## COEVOLUTION OF RHINOXENUS SPECIES

The host cladogram based on host features (Fig. 6) has incongruences with that reconstructed from parasitological data (Fig. 7). A summary of the hypotheses of coevolution of *Rhinoxenus* species and their hosts is presented in the Figure 8. The analysis suggests that cospeciation cannot totally explain host-parasite relationships; events of extinction, dispersion and duplication are also necessary.

Wiley (1988) proposes that absence of parasites in certain host taxa can be associated with three hypotheses: 1) the ancestor of the group was never present in the host and no descendent of this ancestor dispersed to the host; 2) extinction may have occurred within certain host taxon; or



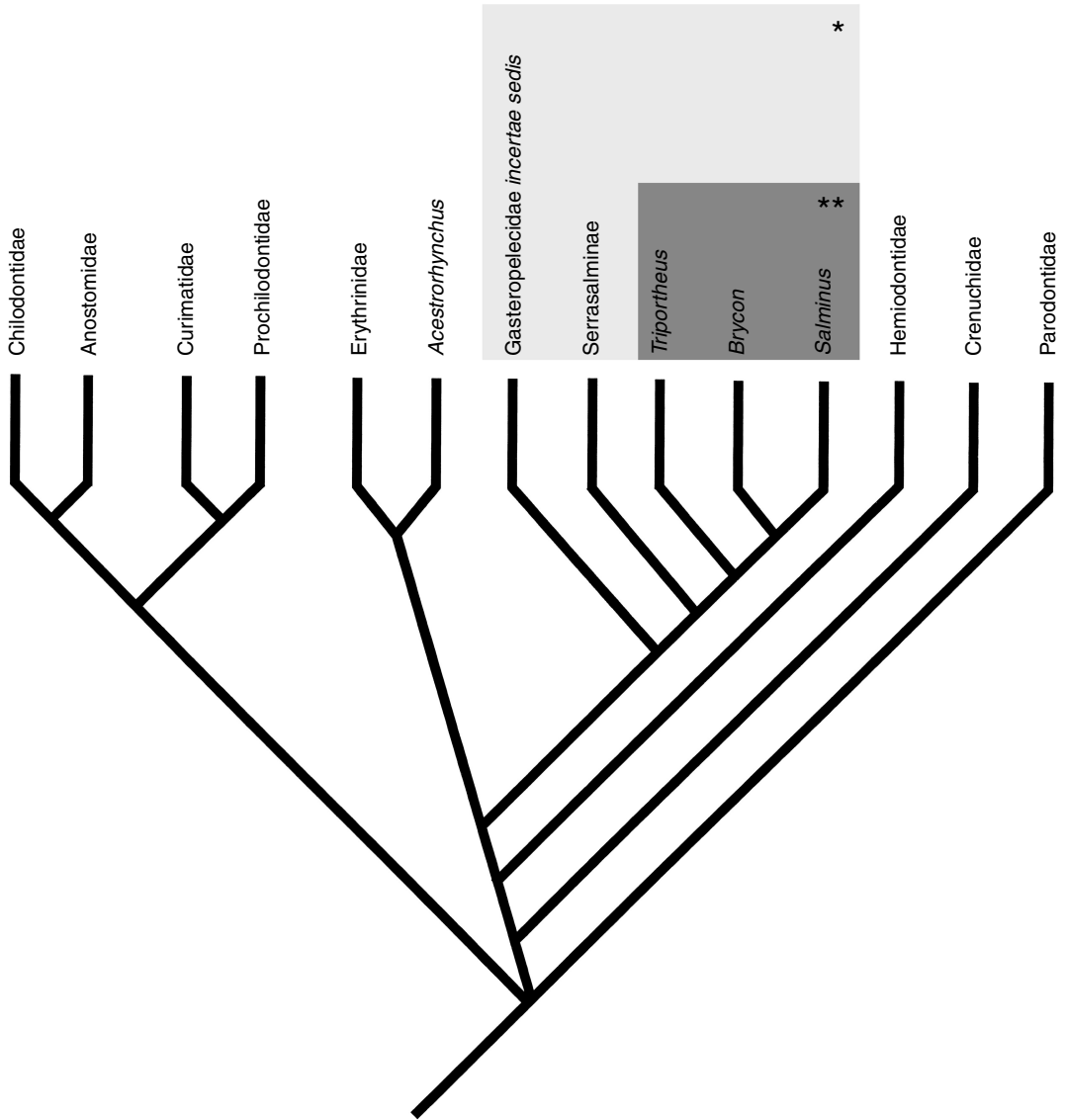


FIG. 6. — Cladogram showing phylogenetic relationship of Characiformes based on morphologic data, after Buckup (1991). The cladogram represents only the families analyzed in the present work. \*, Characoidea (*sensu* Buckup 1998); \*\*, clade *sensu* Malabarba 1998.

respectively. At this level of resolution of the host cladogram, the origin of *R. euryxenus* n. sp. and *R. piranhus* is associated with duplication within

the Serrasalminae. Similarly, *R. anaclaudiae* cospeciated with the ancestor of *Brycon* + *Salminus* + *Triportheus* with subsequent failure to

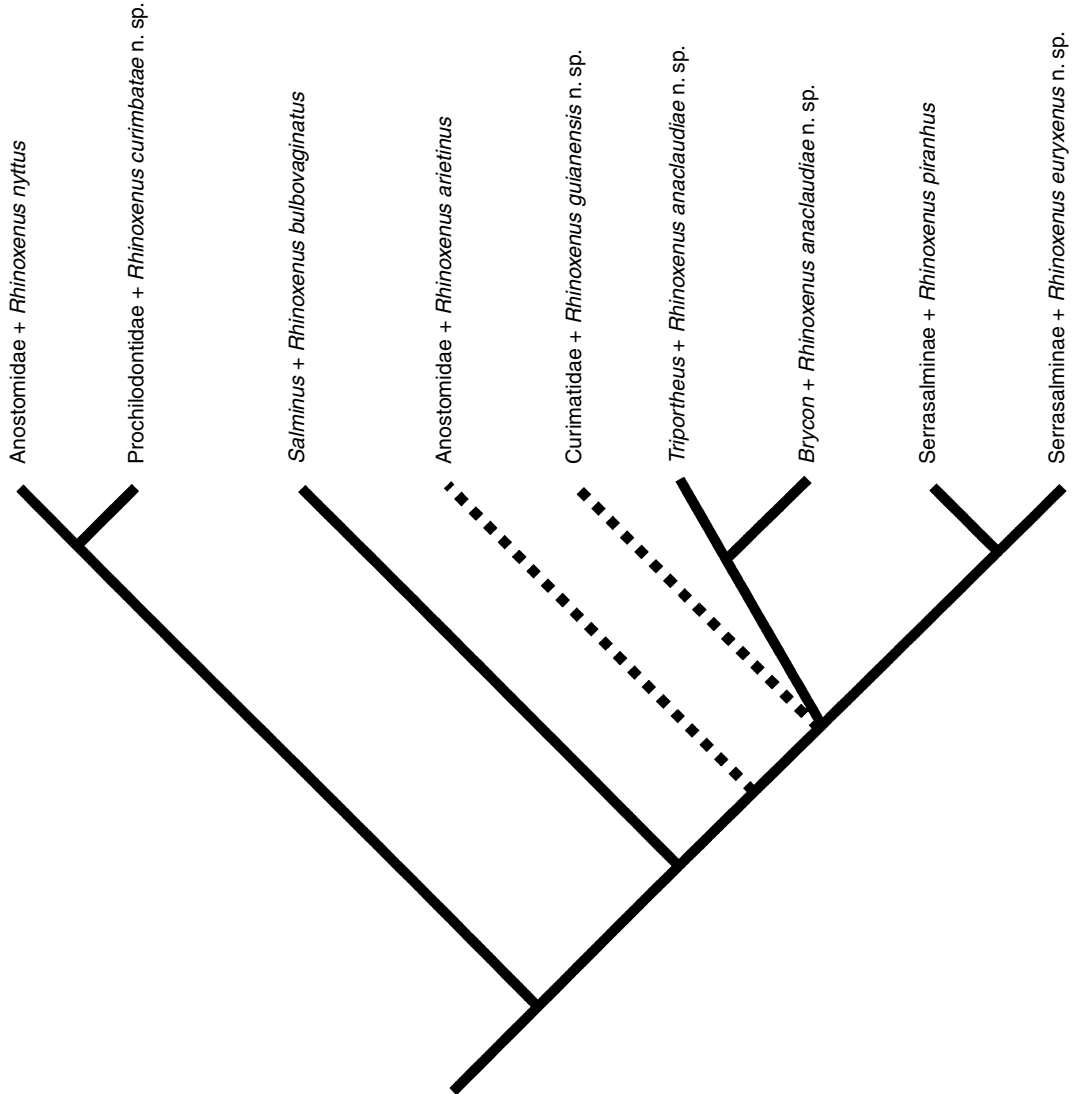


FIG. 7. — Cladogram of hosts groups of *Rhinoxenus* species constructed from parasitological data and using Characiformes taxa analyzed in the present work. Dashed lines postulate dispersion. Each host group is labeled with its taxonomic epithet followed by the *Rhinoxenus* species parasitizing its members.

speciate with the host group (shared with *Triportheus* + *Brycon*) with subsequent extinction in *Salminus*.

Coevolutionary analysis by BPA supports previous hypotheses on the phylogenetic relationships of Anostomidae, Prochilodontidae and Characidae (*sensu* Greenwood *et al.* 1966; Nelson 1996). No parasitological evidence is available to test the sister-group relationships of Chilo-

dontidae, Curimatidae, Erythrinidae, *Acestro-rhynchus*, Gasteropelecidae, Hemiodontidae, Crenuchidae, and Parodontidae since no species of *Rhinoxenus* were collected from fish of these taxa.

Within Characidae, our analysis suggests that Serrasalminae, *Salminus*, *Triportheus* and *Brycon* compose a monophyletic group, supporting the hypotheses of Buckup (1998) and of Malabarba

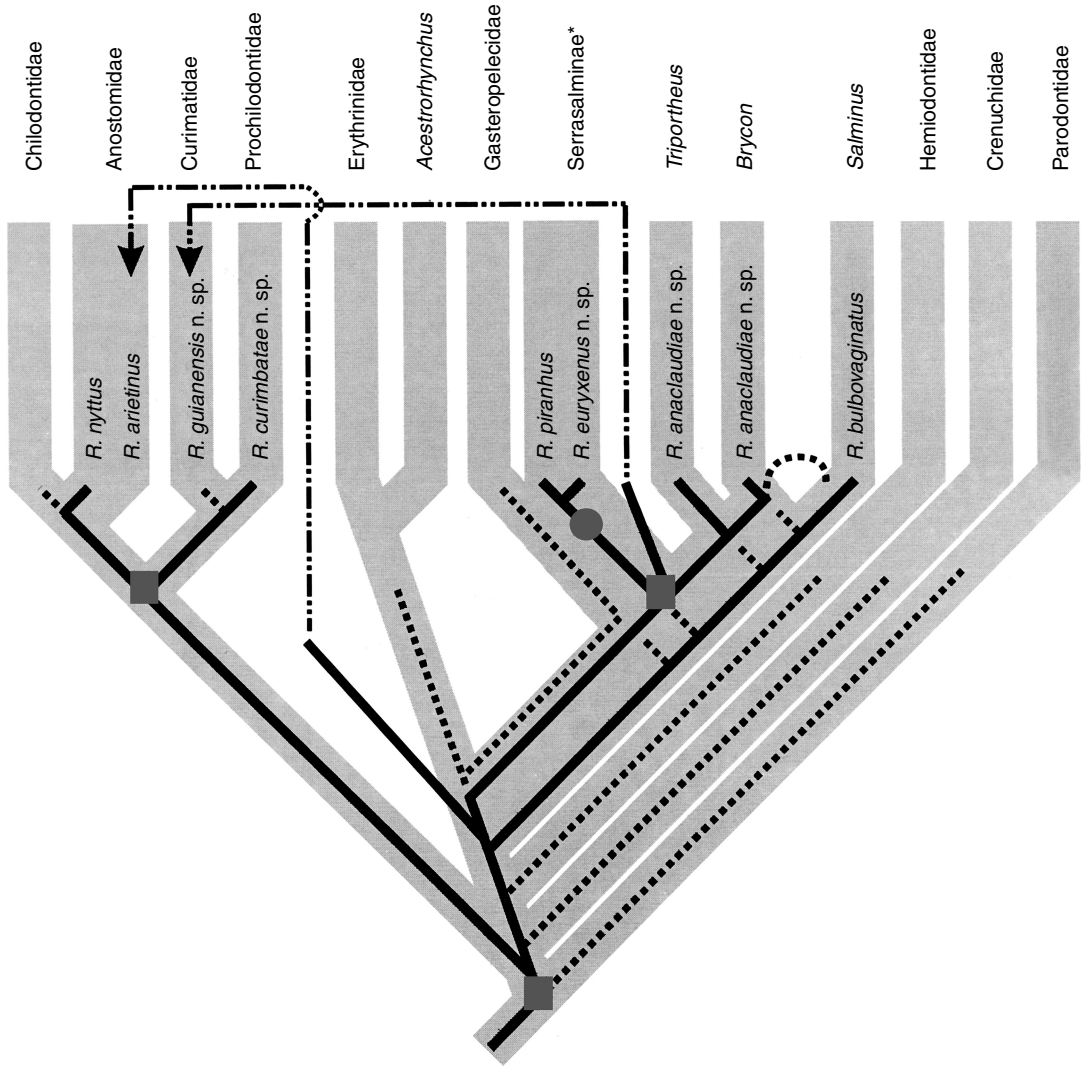


FIG. 8. — Summary of the proposed historical relationships of *Rhinoxenus* species and their hosts. The parasite cladogram (solid lines) is superimposed on that (broad grey lines) of their hosts taxa. Dotted lines indicate postulated extinction or sampling error of parasites; dashed-dotted lines indicate postulated dispersion of parasite clades; circles indicate cospeciation events; triangle indicates duplication event. \*, clade *sensu* Malabarba 1998.

(1998). The phylogeny of fish hosts based solely on parasitological evidence (Fig. 7) suggests that *Brycon* and *Triportheus* are more closely related than to *Salminus*, since both species harbor *Rhinoxenus anaclaudiae* n. sp. Parasites thus support the hypothesis of Castro & Vari (1990), who suggested that *Lignobrycon* (= *Moojenichthys*) and *Triportheus* represent a monophyletic lineage

and this appears more related with a subunit of *Brycon*. However, the current hypothesis of relationships of *Brycon*, *Salminus* and *Triportheus* is that proposed by Malabarba (1998) who suggests that *Salminus* and *Brycon* are more closely related to each other than to *Triportheus*. Based in this hypothesis, the occurrence of *R. anaclaudiae* n. sp. in *Brycon* and *Triportheus* may be associat-

ed with cospeciation followed by extinction in *Salminus*.

The evolution of *Rhinoxenus* appears associated to historical events of the host clade. The origin of many species is linked to cospeciation or dispersion followed by speciation of the ancestor of their respective host family group. Curiously, most *Rhinoxenus* clades subsequently failed to cospeciate within the descendents of their original host species, the ancestor of the respective fish clade. The only apparent exception observed in this study is the clade of parasites of Serrasalminae, with two species, *R. piranhus* and *R. euryxenus* n. sp.

As suggested above, some proposed extinction events are likely artifacts and denser sampling for parasites of members of all characiform families will likely recover species of *Rhinoxenus*. If these putative new findings follow the proposed pattern of parasite distribution, obviously this will reinforce a much more adequate database for additional testing of available host phylogeny.

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## APPENDIX

List of hosts, number of specimens and locality examined during this study. Abbreviations: **AM**, Amazonas; **BR**, Brazil; **FG**, French Guiana; **GO**, Goiás; **MS**, Mato Grosso do Sul; **PR**, Paraná; **TT**, Trinidad-Tobago; \*, specimens collected by researchers of the Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura (NUPELIA-Universidade Estadual de Maringá-Brazil) between 1992 and 1995.

Species	Specimens	Localities
<b>ANOSTOMIDAE</b>		
<i>Leporellus vittatus</i> (Valenciennes, 1850)	4	* Rio Paraná, PR, BR; Rio Tibagi, desembocadura Três Bocas, PR, BR, 24.IV.1997; Rio Tibagi, PR, BR, 29.V.1997
<i>Leporinus agassizii</i> Steindachner, 1876	1	Rio Capucapu, AM, BR, 30.X.1989
<i>Leporinus</i> cf. <i>amblirohynchus</i> Garavello & Britski, 1987	2	Rio Tibagi, desembocadura Três Bocas, PR, BR, 24.IV.1997
<i>Leporinus elongatus</i> Valenciennes, 1849	36	Rio Paraná, PR, BR, 17-19.VI.1996; Rio Tibagi, PR, BR, 24.IV.1997, 28.V.1997
<i>Leporinus friderici</i> (Bloch, 1794)	66	Rio Paraná, PR, BR, 18.VI.1996; Rio Baía, MS, BR, 18.VI.1996; Foz do Iguaçu, PR, BR, 15.XI.1996; Rio Guandu, RJ, BR, 22-25.IV.1991
<i>Leporinus</i> cf. <i>friderici</i> (Bloch, 1794)	1	Rio Tibagi, desembocadura Três Bocas, PR, BR, 24.IV.1997
<i>Leporinus grantii</i> Eigenmann, 1912	3	Iracoubo, Degrad Forian, FG, 8-10.X.1996
<i>Leporinus lacustris</i> Amaral Campos, 1945	64	* Rio Paraná, PR, BR
<i>Leporinus obtusidens</i> (Valenciennes, 1836)	89	Foz do Iguaçu, PR, BR, 15.XI.1996; * Rio Paraná, PR, BR
<i>Leporinus octofasciatus</i> Steidachner, 1915	3	Rio Tibagi, Barra do Ribeirão Tigrinho, PR, BR, 23.IV.1997; Rio Tibagi, desembocadura Três Bocas, PR, BR, 24.IV.1997; Rio Tibagi, PR, BR, 24-28.V.1997
<i>Leporinus striatus</i> Kner, 1858	3	Rio Tibagi, PR, BR, 29.V.1997
<i>Leporinus</i> sp.	1	Rio Tibagi, PR, BR, 29.V.1997
<i>Schizodon altoparanae</i> Garavello & Britski, 1990	38	Rio Paraná, PR, BR; Rio Paraná, PR, BR, 19.VI.1996
<i>Schizodon borelli</i> (Boulenger, 1900)	144	* Rio Paraná, PR, BR
<i>Schizodon nasutus</i> Kner, 1858	9	Rio Tibagi, PR, BR, 24.IV.1997, 28.V.1997
<i>Schizodon</i> sp.	19	Foz do Iguaçu, PR, BR, 15.XI.1996
<b>CHARACIDAE</b>		
<i>Acestrorhynchus guianensis</i> Menezes, 1969	2	Iracoubo, Degrad Forian, FG, 8-10.X.1996
<i>Acestrorhynchus lacustris</i> (Lütken, 1875)	109	* Rio Paraná, PR, BR; Barra do Ribeirão Tigrinho, Rio Tibagi, PR, BR, 23.IV.1997
<i>Aphiocharax</i> sp.	1	Rio Guaporé, AM, BR, no date
<i>Astyanax bimaculatus</i> (Linnaeus, 1758)	55	Fish Farm, Sidrolândia, MS, BR, 3.XI.1996; Barra do Ribeirão Tigrinho, Rio Tibagi, PR, BR, 23, 28.IV.1997
<i>Astyanax fasciatus</i> (Cuvier, 1819)	10	Rio Tibagi, PR, BR, 28-29.V.1997
<i>Astyanax</i> cf. <i>janeiroensis</i> Eigenmann, 1908	2	Rio Guandu, RJ, BR, 25.IV.1991
<i>Astyanax</i> cf. <i>scabripinnis</i> (Jenyns, 1842)	12	Rio Cubatão, PR, BR, 10.V.1996
<i>Astyanax</i> sp.	22	Lagoa Dourada, PR, BR, 27.X.1993; Rio Pequeno, PR, BR, 20.VI.1994; Lagoa da Petrosix, São Mateus do Sul, PR, BR, 21.V.1997
<i>Brycon orbignyanus</i> (Valenciennes, 1850)	24	* Rio Paraná, PR, BR; Fish Farm, Estrada Alexandra-Matinhos, PR, BR, 1996
<i>Bryconamericus stramineus</i> Eigenmann, 1908	90	Foz do Iguaçu, PR, BR, 6.VII.1996, 15.X.1996
<i>Bryconamericus</i> sp.	4	Desembocadura Três Bocas, Rio Tibagi, PR, BR, 24.IV.1997
<i>Characidium lanei</i> Travassos, 1967	120	Rio Cubatão, PR, BR, 10.V.1996; Rio Vitória, PR, BR, 11.V.1996; Rio Peneira, PR, BR, 13.V.1996; Rio Perequê, PR, BR, 4.X.1994, 30.VI.1995, 3.VIII.1995; Rio Dois de Fevereiro, PR, BR, 18.VII.1994, 15.III.1995; Rio Cacatu, PR, BR, 30.VI.1995
<i>Characidium pterostictum</i> Gomes, 1947	14	Rio Cacatu, PR, BR, 30.VI.1995
<i>Characidium</i> sp.	3	Rio Cacatu, PR, BR, 18.VI.1996; Estrada do Lixão, PR, BR, 9.V.1994
<i>Deuterodon gaujo</i> Lucena & Lucena, 1992	7	Rio Cubatão, PR, BR, 11.V.1996

<i>Deuterodon</i> sp.	6	Rio da Venda, PR, BR, 18.VII.1994; Rio Cubatão, PR, BR, 11.V.1996
<i>Galeocharax knerii</i> (Steindachner, 1875)	24	* Rio Paraná, PR, BR
<i>Hollandeichthys multifasciatus</i> (Eigenmann & Norris, 1900)	2	Rio Cubatão, PR, BR, 10.V.1996
<i>Hyphessobrycon</i> cf. <i>bifasciatus</i> Ellis, 1911	10	Rio da Venda, PR, BR, 18.VII.1994
<i>Hyphessobrycon griemi</i> Hoedeman, 1957	12	Rio Perequê, PR, BR, 3.VIII.1995
<i>Hyphessobrycon</i> cf. <i>luetkeni</i> (Boulenger, 1887)	12	Rio Perequê, PR, BR, 3.VIII.1995; Rio Cubatão, PR, BR, 10.V.1996
<i>Hyphessobrycon reticulatus</i> Ellis, 1911	9	Rio Perequê, PR, BR, 2.III.1993, 20.VI.1994
<i>Hyphessobrycon</i> cf. <i>reticulatus</i> Ellis, 1911	1	Unidentified locality
<i>Hyphessobrycon</i> sp.	2	Rio Caracu, PR, BR, 18.VI.1996
<i>Markiana nigripinnis</i> (Perugia, 1891)	2	Rio Miranda, MS, BR, 30.XI.1996
<i>Mimagoniates</i> cf. <i>lateralis</i> (Nichols, 1913)	14	Rio Dois de Fevereiro, PR, BR, 18.VII.1994; Rio da Venda, PR, BR, 18.VII.1994
<i>Mimagoniates microlepis</i> (Steindachner, 1876)	7	Rio Cubatão, PR, BR, 10.V.1996
<i>Mimagoniatis</i> sp.	1	Rio Dois de Fevereiro, PR, BR, 18.VII.1997
<i>Moenkhausia dichoura</i> (Kner, 1858)	18	Rio Cubatão, PR, BR, 10.V.1996; Rio Vitória, PR, BR, 11.V.1996; Rio Guaporé, AM, BR
<i>Oligosarcus hepsetus</i> (Cuvier, 1829)	2	Rio Guandu, RJ, BR, 18.I.1991; Rio Cubatão, PR, BR, 12.V.1996
<i>Oligosarcus</i> cf. <i>hepsetus</i> (Cuvier, 1829)	2	Rio Guandu, RJ, BR, 25.IV.1991
<i>Poptella paraguayensis</i> (Eigenmann, 1907)	3	Rio Miranda, MS, BR, 30.XI.1996; Baía da Medalha, MS, BR, 30.XI.1996
<i>Roeboides prognathus</i> (Boulenger, 1895)	7	Foz do Iguaçu, PR, BR, 15.XI.1996; Baía da Medalha, MS, BR, 1.XII.1996
<i>Salminus brasiliensis</i> (Cuvier, 1816)	4	Rio Paraná, PR, BR; Baía da Medalha, MS, PR, 17.VI.1996
<i>Salminus hillari</i> Valenciennes, 1850	1	* Rio Paraná, PR, BR
<i>Salminus</i> sp.	1	Lagoa Dourada, PR, BR, 27.X.1993
<i>Triportheus</i> cf. <i>nematurus</i> (Kner, 1858)	10	Rio Miranda, MS, BR, 30.XI.1996, 4-5.VIII.1998
<b>SERRASALMINAE</b>		
<i>Colossoma macropomum</i> (Cuvier, 1818)	2	Fish Farm, Pariqueçu, SP, BR, 6.V.1996
<i>Metynnis lippincottianus</i> (Cope, 1870)	2	Lago Miri, Igarapé Taparabu, FG, 15-16.X.1996
<i>Myleus levis</i> Eigenmann & McAtee, 1907	1	* Rio Paraná, PR, BR
<i>Piaractus mesopotamicus</i> (Holmberg, 1887)	24	* Rio Paraná, PR, BR; Farm Fish, Toledo, PR, BR, 11.VII.1994; Fish Farm, Pescobrás, PR, BR, 17.VII.1995
<i>Pristobrycon</i> sp.	1	Rio Capucapu, Cachoeira da Garça, AM, BR, 1.XI.1989
<i>Pristobrycon striolatus</i> (Steindachner, 1908)	2	Rio Jatapu, Maracana, AM, BR, 1-2.XI.1989
<i>Pygocentrus nattereri</i> Kner, 1858	7	Rio Uatumã, AM, BR, 2.XI.1989; Lago da Manga, Igarapé Taparapu, FG, 15-16.X.1996
<i>Serrasalmus altuvei</i> Ramírez, 1965	1	Anavilhanas, AM, BR, 6.VII.1996
<i>Serrasalmus eigenmanni</i> Norman, 1929	1	Rio Jatapu, AM, BR, 1-2.XI.1989
<i>Serrasalmus elongatus</i> Kner, 1858	1	Anavilhanas, AM, BR, 6.VII.1996
<i>Serrasalmus gouldingi</i> Fink & Machado-Allison, 1992	2	Rio Uatumã, Lago Tapana, Santa Anna, AM, BR, 2-3.XI.1989
<i>Serrasalmus marginatus</i> Valenciennes, 1836	148	* Rio Paraná, PR, BR; Rio Paraná, PR, BR, 18-19.VI.1996; Rio Baía, MS, BR, 18.VI.1996; Rio Miranda, MS, BR, 30.XI.1996
<i>Serrasalmus rhombeus</i> (Linnaeus, 1766)	15	Rio Jatapu, AM, BR, 2.XI.1989; Rio Pitanga, AM, BR, 11.X.1989; Anavilhas, AM, BR, 11.X.1989; Iracoubo, Degrad Forian, FG, 8-10.X.1996; Serra da Mesa, GO, BR, 11.VIII.1996
<i>Serrasalmus</i> cf. <i>serrulatus</i>	2	Anavilhanas, AM, BR, 7.VII.1989
<i>Serrasalmus spilopleura</i> Kner, 1858	50	* Rio Paraná, PR, BR; Rio Jatapu, Lago Maracana, AM, BR, 1-2.XI.1989; Rio Uatumã, Lago Tapana, Santa Anna, AM, BR, 2-3.XI.1989; Rio Baía, MS, BR, 18.VI.1996; Lago Miti, Igarapé Tapana, GF, 15-16.X.1996
<i>Serrasalmus</i> sp.	1	Represa Xavantes, SP, BR, 17.IV.1995
<b>CHILODONTIDAE</b>		
<i>Chilodus punctatus</i> Müller & Troschel, 1844	9	Aquarium

<b>CYNODONTIDAE</b>		
<i>Rhaphiodon vulpinus</i> Spix & Agassiz, 1829	76	Rio Paraná, PR, BR, 18.VI.1996; Rio Baía, MS, BR, 17-18.VII.1996
<b>CURIMATIDAE</b>		
<i>Curimata cyprinoides</i> (Linnaeus, 1766)	3	Iracoubo, Degrad Forian, FG, 8-10.X.1996
<i>Cyphocharax gilbert</i> (Quoy & Gaimard, 1824)	4	Rio Guandu, RJ, BR, 22.IV.1991
<i>Cyphocharax nagelli</i> (Steindachner, 1881)	29	* Rio Paraná, PR, BR
<i>Cyphocharax santacatarinae</i> (Fernández-Yépez, 1948)	6	Rio Cubatão, PR, BR, 12-13.V.1996
<i>Cyphocharax</i> sp.	11	Fish Farm, Sidrolândia, MS, BR, 3.XII.1996
<i>Steindachnerina argentea</i> (Gill, 1858)	8	Rio Rouca, TT
<i>Steidachnerina brevipinna</i> (Eigenmann & Eigenmann, 1889)	2	Baía da Medalha, MS, BR, 30.XI.1996
<i>Steidachnerina insculpta</i> (Fernández & Yépez, 1948)	89	* Rio Paraná, PR, BR; Barra do Ribeirão Tigrinho, Rio Tibagi, PR, BR, 23-24.IV.1997; Desembocadura Três Bocas, Rio Tibagi, PR, BR, 24.IV.1997; Rio Tibagi, PR, BR, 28-29.V.1997
<b>ERHYTHRINIDAE</b>		
<i>Hoplias malabaricus</i> (Bloch, 1794)	192	Lagoa Dourada, PR, BR, 26.X.1993; Rio Cubatão, PR, BR, 11.V.1996; Rio Baía, MS, BR, 17.VI.1996; Rio Paraná, PR, BR, 18.VI.1996; * Rio Paraná, PR, BR; Iracoubo, Degrad Forian, FG, 8-10.X.1996; Rio Guandu, RJ, BR, 25.IV.1997
<i>Hoplias</i> cf. <i>malabaricus</i> (Bloch, 1794)	6	Represa Voçoroca, PR, BR, 16.IV.1998; Rio Piraquara, PR, BR, 28.IV.1998; Rio Pequeno, PR, BR, 8.VI.1998
<i>Hoplias</i> sp.	16	Rio Piraquara, PR, BR, 2.III.1993, 22.IV.1994; Rio Dois de Fevereiro, PR, BR, 18.VII.1994; Rio da Venda, PR, BR, 18.VII.1994; Rio Perequê, PR, BR, 4.VII.1994, 6.IX.1994; Represa Capivari-Cachoeira, PR, BR, 14.III.1995; * Rio Paraná, PR, BR
<i>Hoplerethrinus unitaenatus</i> (Agassiz, 1829)	10	* Rio Paraná, PR, BR
<b>GASTROPELECIDAE</b>		
<i>Carnegiella striagata</i> (Günther, 1864)	2	Aquarium
<i>Gasteropelecus levis</i> (Eigenmann, 1909)	11	Aquarium
Unidentified specimen	3	Ilha de Marchantaria, AM, BR, no date
<b>HEMIODONTIDAE</b>		
<i>Hemiodus orthonops</i> Eigenmann & Kennedy, 1903	2	Baía da Medalha, MS, BR, 1.XII.1996
<i>Hemiodopsis microlepis</i> (Kner, 1858)	5	Furo do Catalão, AM, BR, 5.I.1989
<b>PARODONTIDAE</b>		
<i>Apareiodon affinis</i> (Steindachner, 1879)	9	Desembocadura Três Bocas, Rio Tibagi, PR, BR, 24.IV.1997; Rio Tibagi, PR, BR, 28-29.IV.1997
<i>Apareiodon</i> cf. <i>affinis</i>	3	Desembocadura Três Bocas, Rio Tibagi, PR, BR, 24.IV.1997
<i>Parodon nasus</i> Kner, 1859	2	Desembocadura Três Bocas, Rio Tibagi, PR, BR, 24.IV.1997
<b>PROCHILODONTIDAE</b>		
<i>Prochilodus lineatus</i> (Valenciennes, 1836)	252	* Rio Paraná, PR, BR; Represa Capivari-Cachoeira, PR, BR, 16.XII.1994, 13.III.1995, 23.V.1995, 6.VI.1995, 26.X.1995; Rio Paraná, PR, BR, 17-19.VI.1996; Rio Baía, PR, BR, 17-18.VI.1996, Foz do Iguaçu, PR, BR, 15.XI.1996; Barra do Ribeirão Tigrinho, Rio Tibagi, PR, BR, 23.IV.1997; Desembocadura Três Bocas, Rio Tibagi, PR, BR, 24.IV.1997; Rio Tibagi, PR, BR, 28-29.V.1997
<i>Prochilodus</i> sp.	6	Fish Farm, Bocaiúva do Sul, PR, BR, 7.VIII.1997; Fish Market, PR, BR, 12.VIII.1997